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OAT HYBRIDS TO LOOSE AND
COVERED SMUT

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NUBBIN, A COMPOUND CHROMOSOMAL TYPE IN *DATURA**

BY ALBERT FRANCIS BLAKESLEE

*Department of Genetics, Carnegie Institution of Washington
Cold Spring Harbor, N. Y.*

CONTENTS

	Page
Introduction	1
Breeding behavior	4
Morphology	10
The Buckling Group.....	11
The Rolled Group.....	13
The Echinus Group.....	14
Morphology of Nubbin.....	14
Pinched and Hedge.....	17
Chromosomal diagrams of Pinched, Hedge and Nubbin.....	21
Discussion	26
Summary	26
Bibliography	28

INTRODUCTION

Nubbin is one of the mutant types of the Jimson Weed (*Datura Stramonium*) which has been shown (5) to have a single extra chromosome.¹ It was found in 1921 among the offspring of a plant which had been treated by Dr. C. Stuart Gager with radium emanation² and has not appeared spontaneously since. Its parent was a normal (2n) diploid in Line 1 which had been inbred by selfing for nine generations. It was soon recognized as belonging to a category of chromosomal types distinct from anything known in *Datura*, but an analysis of its chromosomal constitution was not possible at that time, for some understanding had first to be gained of the factorial constitution of individual whole chromosomes or of half chromosomes. The analysis which now appears possible may be of interest, we trust, outside of *Datura*, since it shows

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¹ Throughout this paper the bibliographical references are designated by an italicized number in parentheses. The author and title of the paper may be ascertained by referring to the corresponding number in the Bibliography.

² Cf. Proc. Nat. Acad. of Sci., 1927, XII, pp. 75-79.

that permanent unions may occur between portions of non-homologous chromosomes. It will be desirable to give a *résumé* of what we already know about whole and half chromosomes and their arrangement in *Datura*, in so far as this may apply to the Nubbin problem. Some of this

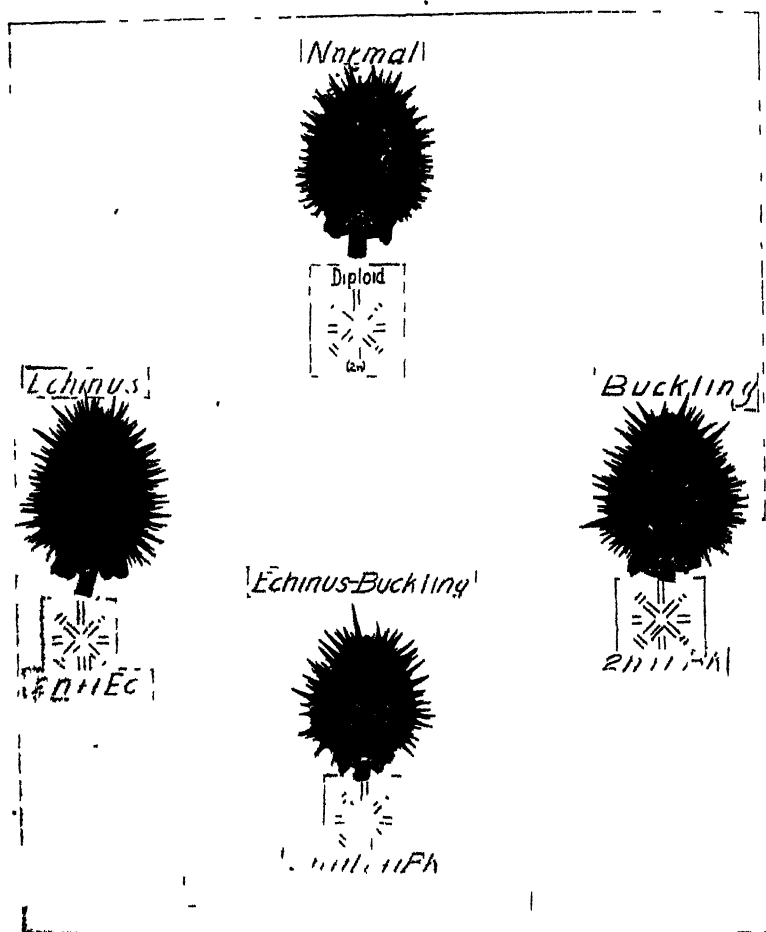


FIG. 1.—The double mutant type—Echinus-Buckling

(capsule of normal diploid ($2n$) above; capsule of Buckling ($2n + 1 Bk$) at right; capsule of Echinus ($2n + 1 Ec$) at left; capsule of double mutant Echinus-Buckling ($2n + 1 Ec + 1 Bk$) below. Underneath each capsule is given its chromosomal diagram.

matter has been printed in detail or outlined in earlier papers, but much is here published for the first time. All the numbered figures are new. The data presented in the tables are, for the most part, entirely

new or form a considerable addition to that previously given. Moreover, since they are almost entirely confined to Line 1 or Line 1A, which latter subline traces its origin to a single haploid 1A (16, 3, 14), the data are much more closely comparable than any hitherto available.

A normal diploid ($2n$) plant of *Datura* has twenty-four chromosomes arranged in sets of two each (14, Fig. 1). Any departure from the normal balanced $2n$ condition shows itself in a more or less marked alteration in the morphology of the plant affected. The various chromosomal types have been discussed in earlier publications (Cf. citations in the Bibliography) and a series of diagrams given (14, Fig. 2) of some of those which have been identified. In these diagrams the relative sizes of the chromosomes are based upon measurements made by Dr. Belling, who has been able to establish six size classes for the twelve individual chromosomes (2). The evidence is very clear that whatever the size of the chromosome, each contains a different assemblage of factors determining the make-up of the whole plant.

The effects of extra chromosomes have been most carefully studied in the ($2n + 1$) types and eleven of the theoretically possible twelve primary forms have been identified, each possessing a single extra unmodified chromosome in a different set.

Figures have already been published (8, 14) showing the modification of capsule form due to the different extra chromosomes. Similarly the leaves, flowers and other parts of the plant are altered by the presence of extra chromosomes and, by the unbalancing effects which they produce, it has been possible to reach conclusions as to the factors present in each individual chromosome. The relative unbalance exerted by one, two, or three extra chromosomes in the same set shown in Pl. I, as well as the resultant effects of a single extra chromosome in each of two different sets in double mutant types shown in Fig. 1, has been discussed elsewhere (8, 14). Not only may one weigh the effects of extra whole chromosomes, but also, as shown by secondary mutant types to be discussed later, the effects of extra half chromosomes (4, 7, 8, 10). At reduction division the extra chromosome goes to half of the daughter nuclei in the formation both of pollen grains and egg cells. The pollen tubes with the extra chromosome, it has been shown by Dr. Buchholz, grow more slowly than those with the normal complement (20), a fact which explains why the extra chromosome is rarely transmitted through the pollen parent and why in consequence there is no essential difference in the proportions to which a ($2n + 1$) type breeds true whether selfed or crossed with pollen of a diploid. The egg cells and zygotes with the extra chromosome, due to the unbalance which the latter exerts, are

less viable than normals, and as a result only about one quarter of the offspring of a $(2n - 1)$ type are like its parent (10).

With the foregoing brief reference to the more common chromosomal types in *Datura*, let us compare Nubbin with other mutants.

BREEDING BEHAVIOR

Like other $(2n - 1)$ forms, Nubbin does not breed true, being not at all transmitted through the pollen and transmitted through the egg

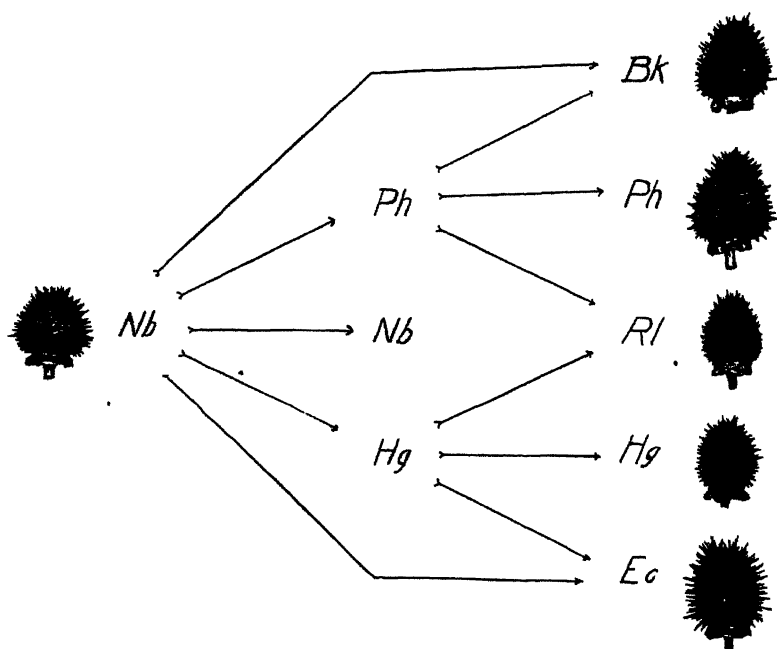
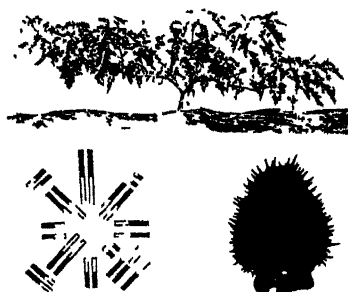


FIG. 2.—Diagram with capsules illustrating the breeding behavior of Nubbin, Plucked and Hedge

The arrows point to the recurrent types thrown in their offspring by these mutants. The normal $(2n)$ offspring are not shown in the diagram. For ratios within line 1 see Table 1.

cells to considerably less than the 50 per cent theoretically possible. It differs from the other $(2n - 1)$ forms in the types which it throws in its offspring, as shown in Fig. 2, in which arrows point to capsules of the types of offspring produced. The normal $(2n)$ offspring are omitted from the diagram. Nubbin (Nb) regularly throws Nubbins, but in addition two other new types with single extra chromosomes,

A Primary (2n+1) Mutant
Buckling



Its Two Complementary Secondary Mutants

Strawberry

Maple



FIG. 3. -Chromosomal diagrams of types in the Buckling group together with habits and capsules

To distinguish the two halves of the chromosomes in the diagrams, one half is shaded and the other left white. The extra chromosome in Buckling is like the other two members in the set. In the secondary, Strawberry, however, the extra chromosome consists of two white halves, while in the complementary secondary, Maple, the extra consists of two shaded halves. Each complementary secondary, therefore, has two extra "doses" of the factors in one half of the Buckling chromosome (a different half for each secondary), while being normal diploid for the factors in the other half. The primary, having one extra dose of the factors in both halves, shows characters represented in each secondary and is intermediate between them in appearance.

Pinched (Ph) and Hedge (Hg), which have never appeared spontaneously in our cultures. Nubbin also throws a few of the primary ($2n - 1$) types, Buckling (Bk) and Echinus (Ec). Pinched throws Pinched, Buckling and the primary ($2n + 1$) Rolled (Rl), while Hedge throws Hedge, Echinus and Rolled. Table 1 gives the offspring of Nubbin, Pinched and Hedge within Line 1. These types have been bred from, rather extensively when heterozygous for different Mendelian factors, and the data thus obtained, though less comparable than those from Line 1, are more extensive and of considerable value in helping to establish the breeding behavior shown in Fig. 2.

Certain conclusions may be reached from a consideration of the data summarized in Fig. 2. In the first place, Nubbin cannot be a primary ($2n - 1$) form in which the extra chromosome is similar in make-up to the other two members of the set, since (a) primary types do not regularly throw other specific mutants (10) and (b) primaries are regularly thrown by triploids (10), while Nubbin is not. Data on the offspring of triploids which were heterozygous for different lines have already been published. Tables 2 and 3 give the data for Line 1A and are, therefore, more nearly comparable, since all the plants trace their origin to the same haploid 1A (14, 16). Further, Nubbin cannot be a secondary, since secondaries throw, in addition to themselves, only their own primaries in any regular proportions. The main points of distinction between primary and secondary ($2n + 1$) types have been outlined elsewhere (4, 10) and a table was given to show the breeding behavior of these types as then known. The data were taken from material derived from a number of different lines. In Tables 4 and 5 the data are more closely comparable, since they furnish a summary of the breeding behavior of plants which, with few exceptions, belong entirely to the highly inbred Line 1. The majority of these parents trace their origin to a single haploid, 1A (3, 14, 16). The few secondaries which do not belong to Line 1 have been repeatedly back-crossed to Line 1A.

Buckling bears the same relation to Pinched that Echinus does to Hedge. Buckling and Echinus are both thrown by Nubbin and hence bear the same relation to Nubbin.

Could the occurrence of Pinched and Hedge be explained in some other way, the fact that Nubbin throws both Buckling and Echinus might lead us to consider it a double mutant, Echinus-Buckling, with an extra chromosome in both the Echinus and in the Buckling set. Even if the chromosomal counts would permit us to consider Nubbin a ($2n + 1 + 1$) mutant, the proportion of types in its offspring is unlike that from a double mutant. Fig. 1, as well as Pl. V, shows the double

TABLE 1
Offspring of Nubbin, Pinched and Hedge from selfings or from back-crosses to Line 1—Garden Records
Figures in parentheses represent percentages of occurrence of Nubbin and related types

[illegible]

mutant Echinus-Buckling and Table 6 gives its offspring. In the progeny of Echinus-Buckling, diploids, the two ($2n + 1$) types and the double type average a rough approximation to a 6 : 2 : 2 : 1 ratio, which we have found in the offspring of other double mutants. It will be noted that Echinus-Buckling throws fewer double mutants than it does the simple mutants Echinus and Buckling, while Nubbin throws more Nubbins than it does Buckling or Echinus types.

From Fig. 2 it will be seen that, although Nubbin itself does not throw Rolled, it is related in some way to Rolled through the fact that both the reciprocal mutants, Pinched and Hedge, throw Rolled. Pinched and Hedge are also morphologically related reciprocally to the two secondaries of Rolled, as will be shown later. Nubbin is related to Rolled in still another way, through its behavior when heterozygous for "B" whites. It has been pointed out that when all the primary ($2n + 1$) types are rendered heterozygous for certain white-flowered lines, called "A" whites, the mutant type Poinsettia alone gives trisomic ratios in its offspring, indicating (17) that the factors for purple and white are located in the Poinsettia chromosome. When, however, these same primaries are heterozygous for certain other white lines called "B" whites, trisomic ratios are thrown by Rolled as well as by Poinsettia (Table 7). The responsibility for the ratio abnormalities has been traced to the Rolled chromosome (11), and a hypothesis in explanation has been offered by the cytological investigations of Dr. Belling (5). It will be sufficient to show by the sample ratios in Table 7 that Nubbin, when heterozygous for "A" whites, gives normal disomic ratios, whereas when it is heterozygous for "B" whites it throws a considerable excess of whites in its offspring. The distinction is so clear that Nubbin is used as a tester in our routine classification of the white lines in our collection into "A" and "B" whites.

MORPHOLOGY

The foregoing conclusions have been drawn from the breeding behavior of Nubbin and its related mutants, Pinched and Hedge, and have prepared the way for an attempt to analyze these mutants by the morphological peculiarities which they show. It will first be necessary to point out some of the characteristics of the related types, the chromosome constitution of which has already been determined. For comparison with the types to be discussed in a moment, photographs of a normal ($2n$) diploid from 1A are given in Pl. IV, A.

THE BUCKLING GROUP

The Buckling group consists of the primary Buckling (Pl. II, A) and of the secondaries Strawberry (Pl. II, B) and Maple (Pl. II, C). The extra chromosome in Buckling is like the other two members of the Buckling set. In the secondaries, however, the extra chromosome is a double half chromosome. Speaking in terms of the conventionalized diagram of Fig. 3, the extra chromosome of Strawberry is made up of two "white"

TABLE 5
Offspring of Primary and Secondary (2n + 1) Types
Summary of Table 4, giving percentages

Parents	Related (2n + 1) Types		% Unrelated (2n + 1) Types	Totals
	% Primaries	% Secondaries		
GLOBE.....	29.05	—	.52	1146
POINSETTIA.....	29.71	.11	.98	922
Dwarf.....	7.09	20.24	1.21	578
COCKLEBUR.....	26.39	.11	1.45	894
Wedge.....	.89	19.26	1.78	784
ILEX.....	32.03	—	.59	668
ECHINUS.....	30.98	.11	.79	881
Mutilated.....	9.56	14.59	1.16	774
ROLLED.....	20.11	.53	2.53	1895
Sugar-loaf.....	2.64	20.44	.79	1780
Polycarpic.....	2.82	2.22	.34	1172
REDUCED.....	18.69	.18	1.3	1075
Scalloped.....	3.69	22.36	.92	541
BUCKLING.....	30.98	.1	1.02	981
Strawberry.....	6.12	31.71	2.82	637
Maple.....	.26	24.08	.13	1524
GLOSSY.....	23.39	0.0	.14	718
Smooth.....	4.1	10.36	.64	463
MICROCARPIC.....	28.59	—	.86	1042
ELONGATE.....	10.81	0.0	.46	657
Undulate.....	1.02	24.52	.13	787
Average for Primary Parents.....	25.52	.14	.97	
Average for Secondary Parents.....	3.82	18.98	.99	
Average for 2n Parents.....16	3654

halves, while the extra chromosome of its complementary secondary is made up of two "shaded" halves. It is for this reason that in this, as in other groups, the primary is intermediate in characters between its two complementary secondaries, having extra both a white and shaded half. The secondaries, on the other hand, are extreme in certain characters having the factors in one half chromosome doubled and the factor

TABLE 6

*Offspring of the Double (2n + 1 + 1) Type Echinus-Buckling
Garden Records of 1924 and 1926*

Pedigree No.	Total	(?)	2n	Bk	Ec	Ec-Bk	Ix	Mc-Bk
230149	103	2	57	21	18	3	1	1
250440	156	3	82	26	29	16		
Totals... ..	259	5	139	47	47	19	1	1

TABLE 7

Summary of the Results of Male Back-crossing to Whites, the Types Poinsettia, Rolled and Nubbin, rendered heterozygous for the "A" White Lines 2 and 33, and for the "B" White Lines 21 and 36

Poinsettia parents, when thus heterozygous for "A" whites, give, in offspring from male back-crosses, trisomic ratios of 2 purples (P) to 1 white (p). Rolled and Nubbin, when heterozygous for "A" whites, give 1:1 ratios. Both Poinsettia and Rolled, when similarly heterozygous for "B" whites, throw purples and whites in proportions approaching trisomic ratios, and Nubbin throws a high excess of whites. Ratios to 1 are in parentheses. Extensive data have been published elsewhere (17), establishing the typical trisomic ratios obtained from Poinsettia parents when heterozygous for the "A" white line 2.

Type of male parent		Poinsettia		Rolled		Nubbin	
Line No.	Class	P	p	P	p	P	p
26	A	111 (1.79)	62 (1)	94 (1.17)	82 (1)	106 (1)	115 (1.08)
33	A	128 (1.91)	67 (1)	73 (.96)	76 (1)	213 (1)	235 (1.10)
21	B	271 (2.23)	121 (1)	184 (1.85)	99 (1)	102 (1)	519 (5.08)
36	B	780 (2.60)	300 (1)	215 (1.95)	110 (1)	61 (1)	408 (6.68)

in the other half as in normal 2n plants. By taking stock of the peculiarities of the three types in this group, we can learn what are the aggregate of factors not only in the whole Buckling chromosome, but also in its two halves. Thus we conclude that the Strawberry half of Buckling contains factors tending to make the plant erect, the stems and corolla dark, the stigma green, the leaves relatively narrow and the capsule short and wide, while if we consider Maple to be a secondary of

July 6, 1927. Supplemental note to be added to footnote 3. Records of the inheritance of the Mendelian characters Bronze and ferox white so far obtained seem to indicate that Maple may be related to the other primary Glossy.

Buckling, as appears to be the case,³ the Maple half of Buckling contains factors for spreading habit, pale stem and corolla, purple stigma and broad leaves. Some of these characters are shown in the appended photographs. The primary Buckling is intermediate in respect to all these characters, as well as others not mentioned, including the internal structure of the peduncle worked out by Dr. Sinnott (21).

THE ROLLED GROUP

The primary Rolled, with its two secondaries, Sugarloaf and Polycarpic, forms another group. As may be judged by the photographs (Pl. III, A, B, C, and Fig. 5), the Sugarloaf half chromosome contains factors for spreading habit, large wedge-shaped capsules with short, thick spines, and moderately wide leaves, while the Polycarpic half has factors for small but erect habit, small elliptical capsules with more slender spines and very narrow leaves. One of the most striking peculiarities of the Sugarloaf capsule is the presence of a set of thick, short spines at the apex which overlap and interdigitate like the teeth at the mouth of a sea-

³As already pointed out (10), one of the characteristics of a secondary, whereby it may be placed in the proper group, is the fact that it throws its own primary in higher proportions than it does any other chromosomal type. As may be seen from Tables 4 and 5, Maple throws a somewhat smaller proportion of Bucklings than might be expected, although more than of any other type. Additional breeding records from Maples heterozygous for various lines give, in over two thousand offspring, the following primaries: 11 Bucklings, 1 Cocklebur, 1 Glossy, 1 Poinsettia, 2 Microcarpics, and 1 double mutant, Maple-Globe. The breeding data, therefore, favors the belief that Maple is, in fact, a secondary of Buckling. So far as many of its most conspicuous morphological characters are concerned, it certainly appears to be on the opposite side of Buckling from Strawberry. In certain characters, however, it shows resemblance to another primary, a single secondary of which is known. This secondary is weak in growth and none of the plants came through in the garden during the present season, so that a close analysis could not be made to determine if possibly it could be complementary to Maple. It should be pointed out that aggregates of factors such as are contained in whole and half chromosomes do not always produce strictly blending effects when present in excess. Thus, in the double type Echinus-Buckling, the thickness of the long, thick stigma of Echinus and the relative shortness of the Buckling stigma are dominant, producing a relatively short but thick stigma of distinctive form in Echinus-Buckling. It is hoped that by another year a closer analysis may be possible of the morphological resemblance of Maple to the other primary, and that Mendelian factors, the trisomic inheritance of which is being investigated, may leave no doubt to our present belief that Maple is a secondary of Buckling. A secondary of Buckling, if complementary to Strawberry, would be expected to show the conspicuous characteristics mentioned in the text above. The classification of Maple, however, has no direct bearing upon the Nubbin problem. The present note is added in view of the possibility that later evidence may show that the Maple half chromosome contains a portion of another chromosome in its make-up. Such a possibility in the evolution of chromosomes is not to be overlooked, in view of the evidence given in regard to the nature of secondaries (4), the occurrence of "A" and "B" whites (5, 11) and of lines which, when crossed together, give 50 per cent abortion in pollen and ovules in the F₁ generation (19), as well as the evidence regarding the chromosome constitution considered in the present paper.

urchin (cf. Pl. VIII). These are lacking in Polycarpic. The stigma of Sugarloaf is large; that of Polycarpic small and its style short. Sugarloaf sets fruit well after pollination, but Polycarpic does so rarely, and it is usually only from potted plants in the greenhouse that fruit has been obtained. In respect to all these characters, the primary Rolled is intermediate.

THE ECHINUS GROUP

Mutilated is the only secondary known in the Echinus group (Pl. IV, B, C), but remembering that primaries are intermediate between their two complementary secondaries, we may predict what the characters of the unknown secondary, when found, will be from the peculiarities of Echinus not shared by Mutilated. This undiscovered secondary we may provisionally call Echinus II. Mutilated is susceptible to a disease usually mutilating the capsule. The capsules, when intact, are rather large with short spines; the leaves are large, dark and thick; the habit erect. The pollen is dimorphic; half of the grains full of starch, like those of normal diploids, and half, presumably those with the extra chromosome, practically devoid of starch (cf. Fig. 4). In appearance Echinus is perhaps more like a diploid than any of the other primaries, but is more erect, has large capsules with long spines, leaves somewhat thicker and larger than normals, and dimorphic pollen like Mutilated. Its pollen dimorphism, as determined by the iodine test, has been used to identify Echinus in the greenhouse, where it is difficult to distinguish before the formation of its long-spined capsules.

MORPHOLOGY OF NUBBIN

Having learned something in regard to the characteristics of the related primary and secondary ($2n + 1$) types, and therefore of the assemblage of factors contained in their extra chromosomes, we may be able to judge what chromosomal components might be responsible for the characters of Nubbin.

Nubbin has distinctly dimorphic pollen, a peculiarity shared only by Echinus and Mutilated. It must, therefore, possess in excess either an Echinus whole chromosome or its Mutilated half, in which the factor or factors for the dimorphism are located. If an extra whole Echinus chromosome is present, there must also be an extra whole Buckling chromosome, since these two primaries have the same relation to Nubbin. This would make Nubbin morphologically the double mutant, Echinus-Buckling. We have already seen from the breeding behavior the difficulties in such a conception. The morphological difficulties are still

greater. The capsules of Nubbin are short, with relatively short spines. Echinus-Buckling is one of the most frequent double mutants to be produced by triploids. Its capsules are large, with long spines (Fig. 1). The factors for large capsules and large spines are apparently dominant in double mutants in which the Echinus chromosome is one of the two

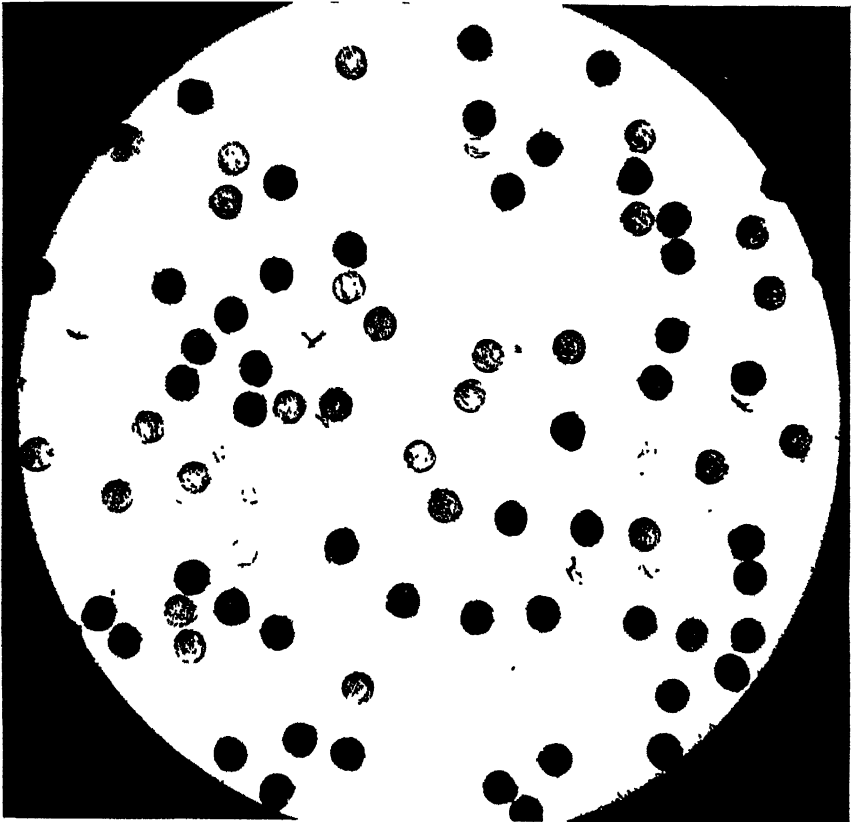


FIG. 4. — Photograph of pollen grains of Nubbin, stained with iodine

Half of the grains, presumably those with the extra chromosome, are practically devoid of starch and stain light, while half are full of starch like those of normal diploids and stain dark. A similar pollen dimorphism in respect to presence of starch is found to be characteristic of Echinus, and also of its secondary, Mutilated.

extras, as seen in the double mutants shown in Pl. V. Other characters of habit, leaf, etc., not readily detectable in a photograph show that Nubbin cannot be Echinus-Buckling. As a class, double mutants are weak plants, due to the unbalance of two extra chromosomes. Nubbin is

more vigorous than Echinus-Buckling and probably more so than any other common double mutant.

Since a whole extra Echinus chromosome is ruled out, Nubbin must contain the Mutilated half chromosome in excess, since both Mutilated and Nubbin have dimorphic pollen. Nubbin is much more vigorous in growth than the mutant Mutilated, which has, as its extra chromosome, two similar halves containing the factors for dimorphism. Hence Nubbin can contain, at most, a single Mutilated half chromosome in excess; otherwise the plant would be more severely unbalanced. As it possesses an extra half chromosome of Echinus, one would expect Nubbin to throw a certain proportion of this primary, as does also the secondary Mutilated.

We have apparently discovered the chromosomal component responsible for the dimorphic pollen in Nubbin and for the relation which Nubbin bears to the primary Echinus. Let us see if we can discover the component responsible for the relation of Nubbin to Buckling. Since half a chromosome was found to be responsible for the relation of Nubbin to Echinus, and Buckling and Echinus are similarly related, we should anticipate that one or the other half of the Buckling chromosome was in excess in Nubbin. Inspection of photographs of the eleven primaries (8, Fig. 4, and 14, Fig. 5; also, Pl. V of this paper) and of their secondaries so far discovered, shown in Pl. VI, reveals that the capsule of Strawberry is most nearly like that of Nubbin in appearance. Nubbin shows none of the characters peculiar to Maple, believed to be the secondary of Buckling and complementary to Strawberry. The capsule form is the most distinct, but not the only character which leads us to conclude that Nubbin has the Strawberry half of the Buckling chromosome in excess. Since Nubbin is more vigorous than Strawberry, there can be only a single Strawberry half chromosome in excess.

Morphologically, Nubbin (Pl. VII, A) seems to be $(2n + 1/2 \text{ Mutilated} + 1/2 \text{ Strawberry})$. Its pollen dimorphism and thickish leaves come from the Mutilated component, while its capsule shape and erect habit are derived largely from the Strawberry component. Naturally the Mutilated and the Strawberry characters are not so well expressed in Nubbin as in the $(2n + 2/2)$ Mutilated and Strawberry types, where the factors in a single half chromosome are doubled. Nubbin, as also Echinus, does not usually have capsules mutilated by disease, as is the case with the mutant Mutilated, probably because the unbalance of more than a single Mutilated half chromosome is necessary to cause susceptibility to the mutilation. Double mutants in which one component is a secondary (Maple-Globe) are not so common as those in which both

components are primaries (*e. g.*, Echinus-Buckling), and we have no records of types in which both components are secondaries. If we should discover such a double mutant as a ($2n + 1$ Mutilated + 1 Strawberry), we should probably have a plant somewhat similar to Nubbin, but much less vigorous and with many of its characters more extreme.

In considering Nubbin to be morphologically ($2n + 1/2$ Mutilated + $1/2$ Strawberry), as we are forced to do, we have not explained the relation of Nubbin to Rolled nor to Pinched and Hedge. The Rolled chromosome has been determined by Dr. Belling to be distinctly the largest of the twelve (1) and either half, as well as the whole chromosome, has a very distinct effect upon the appearance of a plant when present in excess. It seems clear that morphologically Nubbin does not contain an extra Rolled chromosome nor an extra half of this chromosome. A way out of the difficulty may be found by a consideration of the morphology of the reciprocal types—Pinched and Hedge.

PINCHED AND HEDGE

Pinched (Pl. VII, B) was early recognized as similar in appearance to Sugarloaf, one of the secondaries of Rolled, only less extreme. Its leaf shape, capsule form, habit, and several other characters were such that we imagined it might be a Sugarloaf type with only a half instead of two half Sugarloaf chromosomes extra. This conception of Pinched we now believe to be correct, with the addition of the Strawberry half of the Buckling chromosome, already shown to be a component of Nubbin. If it contained, in excess, halves of the Rolled and of the Buckling chromosomes, we should expect it to throw these two primaries, as it does. Morphologically, the extra halves could not possibly be Polycarpic or Maple, the complementary halves to Sugarloaf and Strawberry. Polycarpic would tend to make the habit more erect, the leaves narrower, the stigma smaller, the style shorter, than is the case in Pinched, while Maple would tend to make the habit too spreading, the leaves too broad, the stem and flowers too pale, etc. The specific influence of the Strawberry half chromosome is evident, but the Sugarloaf half has more effect apparently upon the conspicuous characters. Pinched we believe to be correctly represented by the formula ($2n + 1/2St 1/2Sg$) with the two extra halves joined together.

Hedge (Pl. VII, C) is complementary to Pinched, in that it also throws Rolled. It bears a similar relation to Echinus that Pinched bears to Buckling. Hedge can be considered from its morphology to have in excess the Polycarpic half of the Rolled chromosome, joined to the Mutilated half of the Echinus chromosome. The two extra Polycarpic

halves in the secondary ($2n + 2/2$ Polycarpic) bring about an extreme unbalance, dwarfing this type almost out of existence. Only one Polycarpic half in excess must exert considerably less unbalance and, as a result, Hedge resembles Polycarpic less than it does a Rolled minus the Sugarloaf characters. The characters of Mutilated are also extreme and the plant is often of weak growth. As a consequence of the weakening effect of each of its two extra half chromosomes, Hedge is less vigorous than many mutant types. It gets its erect habit of growth from both

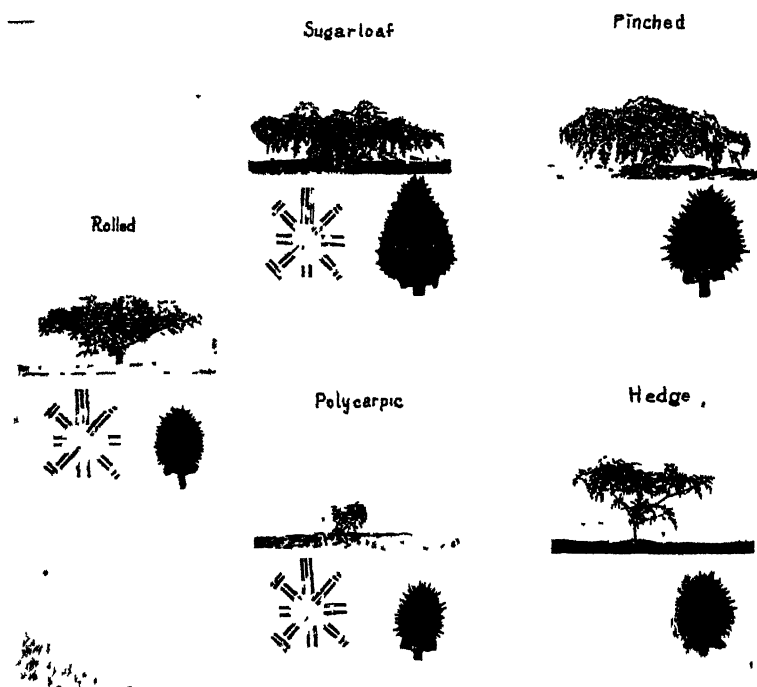


FIG. 5.—Chromosomal diagrams of the Rolled group and comparison of the secondaries, Sugarloaf and Polycarpic, with Pinched and Hedge

Mutilated and Polycarpic, especially the latter; the light color of its leaves and stems and its relatively small leaves it derives from Polycarpic, the slight thickening and increased width of leaves, from Mutilated.

The similarities of Pinched and Hedge respectively to Sugarloaf and Polycarpic are pointed out in Fig. 5.

The apex of the capsule is a convenient character to use in comparing Pinched and Hedge with Rolled and its secondaries, as shown in Pl. VIII.

In Sugarloaf, the thick, short spines at the top of the capsule overlap in a very characteristic manner. In Polycarpic thick apical spines are lacking and those present stand for the most part erect without overlapping. The capsule of Rolled is intermediate in this regard, as would be expected. Top views are given of Sugarloaf and Rolled in the appended photographs, but no capsules were available of Polycarpic the present season. As may be seen from the photographs of Pinched and Hedge, the former resembles Sugarloaf in this capsule character, while Hedge, like Polycarpic, is without thick overlapping apical spines.

As the Mutilated half of the *Echinus* chromosome possesses factors causing the suppression of starch in the pollen grains affected, we should expect the pollen grains of Hedge to be as strongly dimorphic, when tested with iodine, as are the pollen grains of *Echinus*. The pollen dimorphism in Hedge, however, is relatively weak at best and often may not be noticed when grains are examined with iodine. Lack of dimorphism in the pollen grains of Hedge may appear at first sight a serious objection to our conception of its chromosomal constitution. A consideration of the matter of chromosomal unbalance, however, will show us that similar situations to those found in Hedge are to be expected. The balanced $2n$ condition produces $1n$ pollen grains full of starch. In diploids, the *Echinus* chromosome, which in its Mutilated half contains factors tending to suppress pollen starch, cannot show its effect on the $1n$ grains on account of being counterbalanced by one or more other chromosomes which have factors especially favoring starch formation and hence antagonistic to the *Echinus* chromosome, specifically its Mutilated half. The lack of a strong pollen dimorphism in Hedge might be caused by factors in the Polycarpic half which antagonize the factors for suppression of pollen starch in the Mutilated half to which it is joined. If it were possible to obtain the double mutant, Polycarpic-*Echinus*, the assumption of pollenstarch-favoring factors in the Polycarpic half antagonistic to the starch-suppressing factors in the Mutilated half could be proven or disproven. The pollen grains of a Polycarpic-*Echinus* should be: $1n$, $(1n + 1 Ec)$, $(1n + 1 Py)$ and $(1n + 1 Ec + 1 Py)$. If Polycarpic were not antagonistic to *Echinus* (or its Mutilated half), we should expect the $1n$ and the $(1n + 1 Py)$ grains to be dark with starch, while the $(1n + 1 Ec)$ and the $(1n + 1 Ec + 1 Py)$ grains ought to be light-colored and practically free from starch, giving thus the 1:1 ratio of dark to light grains which occurs in pollen of *Echinus* and Mutilated. If, however, antagonism occurs, we should expect the $(1n + 1 Py + 1 Ec)$ to be dark, like $1n$ grains, or, if the antagonism were not complete, to be intermediate in starch content. Instead of a 1 : 1 ratio of darks to

lights we should have 3 darks to 1 light or 2 darks to 1 intermediate to 1 light. Unfortunately, it will probably never be possible to discover a Polycarpic-Echinus plant. Neither Polycarpic nor Echinus carries through the pollen, so the double mutant desired could not be manufactured to order by crossing these two types. Secondaries are not to be expected in the offspring of triploids, a common source of double mutants, and therefore Polycarpic-Echinus cannot be looked for from $3n$ parents. Finally, the unbalance of two extra Polycarpic half chromosomes so nearly kills the plant affected that it is certain the further addition of an Echinus chromosome would render the double mutant sought for non-viable.

While it does not seem possible to obtain direct evidence for or against antagonistic factors in the Polycarpic half chromosome, indirect evidence might be secured regarding the possible antagonism in the whole Rolled chromosome when it is a component of the double mutant type Rolled-Echinus. Rolled is one of the least common types in the offspring of triploids, and we have never found a Rolled-Echinus in sowings from $3n$ parents. This double type, however, we are endeavoring to obtain by the following procedure: The $(4n + 1)$ types are relatively difficult to recognize on account of the slight unbalance exerted by the single extra chromosome over the double number 48 . However, we have found a $(4n + 1)$ Echinus in a tetraploid pedigree and identified it largely by its dimorphic grains. This $4n$ Echinus we have already crossed with a diploid ($2n$). Theoretically, half of the crossed seed which we have ready for planting should give $3n$, and half should give $(3n + 1)$ offspring, the latter with the extra chromosome in the Echinus set. By a similar cross we have obtained a $(3n + 1)$ Globe, the offspring of which were mostly $(2n + 1)$ Globes or double mutants with the Globe chromosome as one of the extras (unpublished data). By obtaining offspring from our $(3n + 1)$ Echinus, if and when we secure it, we hope to have in hand a $(2n + 1)$ Rolled + 1 Echinus, and can then determine by the method suggested above whether or not Rolled is antagonistic to Echinus in respect to pollen dimorphism. This indirect method would be usable only if the Sugarloaf half of Rolled did not more or less completely counterbalance the effects of the Polycarpic half.

As to the effect of the Sugarloaf half on pollen starch, we have no direct evidence. Indirect evidence, however, is available from a series of counts of good and bad pollen grains, made this past summer, in the primary types heterozygous for Line 26, which is a bad pollen inducer (19). In this series were included Nubbin, Pinched and Hedge, but no secondaries. Many of the Pinched and Hedge plants were recorded as

having more or less dimorphic pollen, indicating that the Pinched as well as the Hedge chromosome has a tendency to cause suppression of pollen starch. Unfortunately, it is too late at the present writing to make a careful study of Sugarloaf and Strawberry for the purpose of determining whether the extra chromosomes in these types have a tendency to suppress pollen starch. It has been recognized for some time, however, that Buckling, the primary of Strawberry, has a tendency to pollen dimorphism, as shown in the pollen tests of the offspring of triploids in which Echinus and Buckling, together with the other primaries (but not their secondaries), were to be expected. As will be shown presently, Nubbin is believed to contain both a Pinched and a Hedge chromosome. A tendency, therefore, on the part of the Pinched chromosome, which contains a Sugarloaf and a Strawberry half, to suppress pollen starch would explain the strong pollen dimorphism in Nubbin by its neutralizing the assumed starch-favoring factors in the Polycarpic chromosome. Despite the condition of the pollen, which is the only fact in the morphology or in the breeding behavior that seems at all seriously in conflict with the conception of Nubbin, Pinched and Hedge, as we have outlined it, we believe the chromosomal formula of Hedge may be written $(2n + 1/2Mt + 1/2Py)$ with these two halves united.

CHROMOSOMAL DIAGRAMS OF PINCHED, HEDGE AND NUBBIN

In Figs. 6 and 7 are given diagrams representing our conception of the arrangement of the chromosomes involved in Pinched and Hedge. That, in Pinched, the Sugarloaf half is permanently joined to the Strawberry half, and that in Hedge the Polycarpic half is similarly united to the Mutilated half, seems certain, since otherwise we should expect to discover in their offspring the following types: $(2n + 1/2 Sg)$, $(2n + 1/2 St)$, $(2n + 1/2 Py)$ and $(2n + 1/2 Mt)$. These types should be viable, but they have not been identified. At reduction division the compound chromosome would behave in the same manner as an ordinary extra chromosome at trisomic disjunction, and 1n and Pinched or Hedge egg cells and pollen grains would be formed as indicated by the dotted lines in the diagrams. The method of production of Buckling and Rolled gametes from Pinched is indicated in the diagrams, and a similar method would be responsible for the production of Echinus and Rolled gametes from Hedge.

Fig. 8 represents our conception of the chromosome arrangement in Nubbin. It may be thought of as a double mutant compounded of Pinched and Hedge, but with one normal Rolled chromosome left out.

If it had two normal Rolled chromosomes as well as a Pinched and a Hedge chromosome, which together furnish the two halves of Rolled, it should show Rolled characters, which is not the case, and should also throw Rolled offspring, which it does not do. The two halves of Rolled brought in by Pinched and Hedge prevent the dropping out of a whole Rolled chromosome from causing a factorial deficiency for the Rolled set.

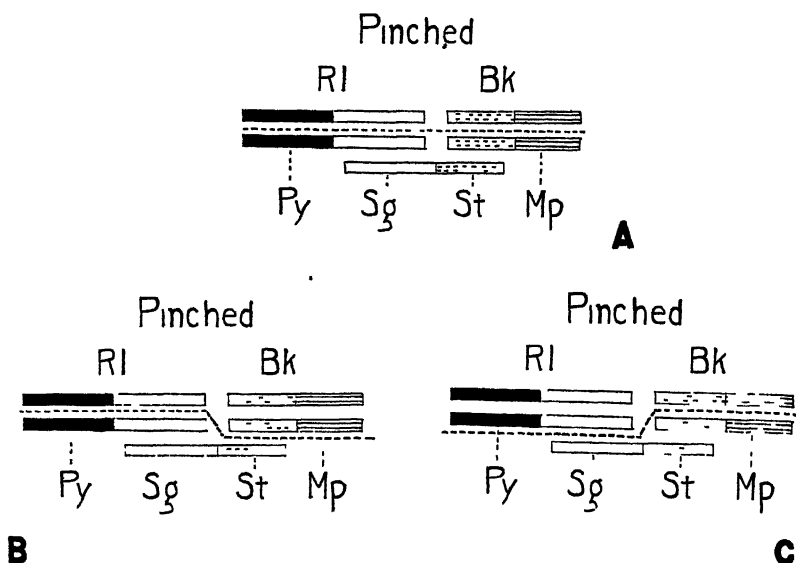


FIG. 6, A.—Diagram of the arrangement of chromosomes involved in Pinched

The dotted line represents the disjunction of chromosomes at reduction, which leads to the formation of $1n$ and Pinched eggs and pollen grains.

FIG. 6, B.—Diagram of Pinched

The dotted line represents the disjunction which leads to the formation of $(1n + 1)$ Buckling and $1n - 1$ Bk + $1/2$ St $1/2$ Sg eggs and pollen grains. The latter cells, since they lack a half of the Buckling chromosome, would probably die and be represented by aborted ovules and pollen grains.

FIG. 6, C.—Diagram of Pinched

The dotted line represents the disjunction which leads to the formation of $(1n + 1)$ Rolled and $1n - 1$ RI + $1/2$ St $1/2$ Sg eggs and pollen grains. The latter cells, since they lack the Polycarpic half of the Rolled chromosome, would probably die and be represented by aborted ovules and pollen grains.

Deficiency for the set of genes in a Rolled chromosome ($1\frac{1}{2}$) would cause a greater unbalance than is shown by the vigorous type Nubbin, as would also the presence of an extra Rolled chromosome in addition to the Mutilated and Strawberry halves shown to be in excess in Nubbin. Although morphologically the factorial constitution of Nubbin may be represented

as $(2n + 1/2 Mt + 1/2 St)$, the formula should be, in terms of the individual chromosomes, $(2n - 1 Rl + 1/2 Mt + 1/2 Py + 1/2 St + 1/2 Sg)$.

In Fig. 8, A, the horizontal dotted line represents the line of division leading to the formation of a normal 1n gamete and a Nubbin gamete. The latter probably has a high viability, since the Nubbin complex is transmitted to a larger proportion of its offspring than other $(2n + 1)$ types (cf. Tables 1, 4 and 5).

Disjunction, however, may separate the chromosomes, as indicated in Fig. 8, B, leading to the formation of a Pinched pollen grain and a cell with the Hedge chromosome, but without a Rolled chromosome. Such a cell would die and form an aborted grain, since it would be deficient for the factors in the Sugarloaf half of Rolled while containing

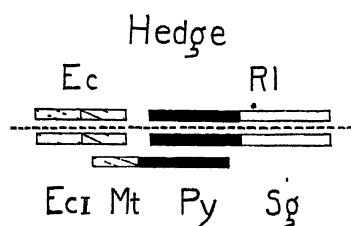


FIG. 7.—Diagram of the arrangement of chromosomes involved in Hedge

Ec II is the half of the Echinus chromosome opposite to Mutilated. A $(2n + 2/2)$ mutant with the Ec II half doubled, which would be the secondary of Echinus, complementary to Mutilated, has not been discovered. The dotted line represents the disjunction which leads to the formation of 1n and Hedge eggs and pollen grains. Rolled and Echinus eggs and pollen grains would be formed by a type of disjunction similar to that shown in figures 6, B and 6, C for the formation of Rolled and Buckling gametes in the mutant Pinched.

in excess the factors in the Mutilated half of Echinus. Similarly, as shown in Fig. 8, C, a Hedge pollen grain may be formed, together with a grain which aborts, since it is deficient for the Polycarpic half of Rolled. We should expect as many aborted grains as there are grains with the constitution of Pinched and Hedge. We should also expect a deficient, and therefore an aborted, grain for each grain with the constitution of either of the primaries, Buckling or Echinus, since, as has been shown (18), secondaries probably owe their relatively high proportion of bad grains largely to their production of primaries. For type of disjunction responsible, see diagrams of Pinched, Figs. 6, B, C. Not all the egg cells with extra chromosomes live to be recorded. Hence the number of Pinched, Hedge, Buckling and Echinus individuals will represent the minimum proportion of bad grains or ovules expected, due to the causes just mentioned. From Table 1 it will be seen that we have 9.1 per cent

of these types in the offspring, not to mention a high proportion of other $(2n + 1)$ types produced presumably by non-disjunction, which would be accompanied by deficiencies.

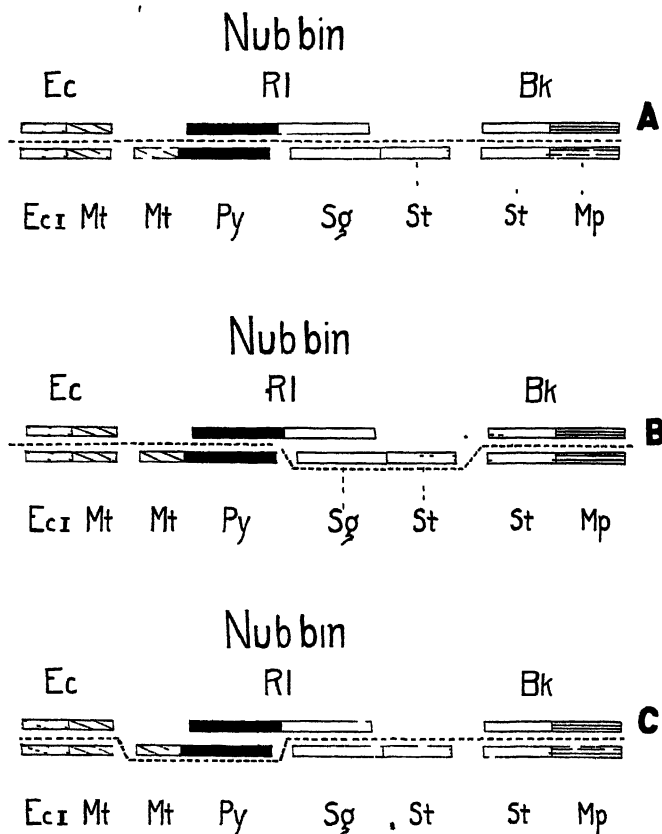


FIG. 8, A.—Diagram of the arrangement of chromosomes involved in Nubbin

Ec II is the half of the Echinus chromosome opposite to Mutilated. The $(2n + 2/2)$ Ec II has not yet been discovered. The horizontal dotted line represents the disjunction which leads to the formation of 1n and Nubbin ($1n = 1 \text{ RI} + 1/2 \text{ Sg} + 1/2 \text{ St} + 1/2 \text{ Mt} + 1/2 \text{ Py}$) eggs and pollen grains.

FIG. 8, B.—Diagram of Nubbin

The dotted line represents the disjunction which leads to the formation of Pinched and 1n — $1 \text{ RI} + 1/2 \text{ Mt} + 1/2 \text{ Py}$ eggs and pollen grains. The latter cells, since they lack the Sugarloaf half of the Rolled chromosome, would abort.

FIG. 8, C.—Diagram of Nubbin

The dotted line represents the disjunction which leads to the formation of Hedge and 1n — $1 \text{ RI} + 1/2 \text{ St} + 1/2 \text{ Sg}$ eggs and pollen grains. The latter cells would be expected to abort. Buckling and Echinus, but not Rolled, gametes could be formed by a type of disjunction indicated under Pinched and Hedge.

In Table 8 are given the percentages of bad grains in Nubbin and related types. It will not be desirable to attempt a too close comparison between the proportion of types thrown by a $(2n+1)$ mutant and the percentage of bad pollen grains, since many factors may be involved. As we have shown (9, 10), environmental influences such as low temperatures may stimulate the production of bad grains in normal diploids and the grains with an extra chromosome appear to have a lessened viability. We believe it is significant, however, and in accord with our interpretation, that Nubbin is shown to have a relatively high proportion of bad grains in comparison especially with Pinched and Hedge, which throw fewer types the formation of which should be accompanied by aborted ovules and pollen grains.

TABLE 8

Percentages of Aborted Pollen Grains in Normal ($2n$) Diploids, Nubbin and Related Mutant Types.

Records of 1924, taken from citation (18), Table 3

Types	2n	Nb	Ph	Bk	St	Hg	Ec	Mt	Rl	Sg	Py
Percentages of aborted grains.	1 5	13 3	6 8	3 4	11 3	6 9	4 6	14 0	3 1	15.4	20.8

From our conception of the chromosomes involved in Nubbin, Pinched and Hedge, one would expect that configurations would be found in this group showing more than three chromosomes attached. Such a condition of attachment of as many as five chromosomes has been discovered, in fact, through Dr. Belling's cytological investigation of these types before the relations offered in the present paper had been worked out, and a figure showing attachment between non-homologous chromosomes in Hedge has already been published (5).

A study of the internal anatomy of the flower stalk in Nubbin and the various related types made by Dr. Sinnott (21), so far as it has been carried, has brought out no facts in opposition to our interpretation of the constitution of these types. There are other facts, not fully analyzed as yet, which also seem to offer confirmatory evidence for the conclusions which are here presented.

Throughout the present paper we have spoken, for convenience, of the Sugarloaf, Polycarpic, Strawberry and Mutilated portions as halves of the respective whole chromosomes of which they form a part. This is not necessarily the case, and a closer analysis of morphological characters

as well as a detailed cytological study of Nubbin, Pinched and Hedge may show that the fracture of chromosomes in the original production of these mutants did not involve the separation of equal parts in all the chromosomes affected. So far, however, as concerns the mass effects of the total assemblage of factors in the portions of chromosomes discussed, as judged by the morphological peculiarities of the secondary types for which they are responsible, we do not believe we are far wrong in considering these portions to be half chromosomes.

DISCUSSION

The results discovered in regard to the chromosomal constitution of Nubbin may have bearing upon general problems of evolution.

It has already been shown that similar segments of two homologous chromosomes may separate from the parent chromosome and become joined in the formation of the double half extra chromosome in $(2n + 2/2)$ secondary types (4). The difference in breeding behavior between "A" and "B" whites may find its interpretation in the hypothesis suggested (5) of segmental interchange between non-homologous chromosomes. The chromosomal constitution of Nubbin, Pinched and Hedge shows that more than a single compound chromosome made up of segments from non-homologous chromosomes may be present in a plant without greatly affecting its vigor of growth. Unpublished data (19 and later records) suggest that in the development of races collected from the wild, segmental interchange between non-homologous chromosomes may have been a not-infrequent phenomenon. We have a number of races which, when crossed with our Line 1, give plants showing 50 per cent abortion of ovules and pollen grains. For one of these lines we have apparently located the cause of the abortion in two non-homologous chromosomes by trisomic ratios in respect to plants with good and plants with 50 per cent bad pollen. In two other lines responsible for abortion in F_1 's with Line 1, apparently different sets of chromosomes are involved in bringing about the gametic sterility.

The solution of the Nubbin problem may contribute toward an understanding of a method of evolution, in that it shows the possibility of alterations in the morphology of a plant being brought about by shifts in large groups of genetic factors contained in the chromosomes.

SUMMARY

It has been shown that the mutant type Nubbin has a single extra chromosome. In its offspring it throws, besides normal diploids, two

new types, Pinched and Hedge, each also with a single extra chromosome. Nubbin throws, in addition, two primary ($2n + 1$) types, Buckling and Echinus. Pinched also throws Buckling as well as itself, and Hedge throws Echinus, while both throw the primary Rolled, which is not thrown directly by Nubbin.

The breeding behavior is described of primary ($2n + 1$) and secondary ($2n + 2/2$) types of *Datura* with extra chromosomes in a single set, as well as of double ($2n + 1 + 1$) types with an extra chromosome in each of two different sets. Considerable new data, closely comparable because chiefly within Line 1A derived from a single haploid, are offered regarding the types of offspring from triploids and from the eleven primaries and their secondaries. An account with illustrations is given of the morphological characters of Nubbin and of the types related to it, and conclusions are reached in regard to the assemblage of factors contained in the halves of the extra chromosomes involved in these types.

Nubbin has dimorphic pollen grains, as have also the primary Echinus and its ($2n + 2/2$) secondary Mutilated. Judging from the breeding behavior and from the morphological characters, Nubbin is considered to have in excess the Strawberry half of the Buckling chromosome and the Mutilated half of the Echinus chromosome in which the factor for pollen dimorphism has been located. To understand the relationship, now evident, of Nubbin to Rolled, shown by the breeding behavior and by the fact that, when heterozygous for "B" whites, it gives abnormal ratios for purples and whites, as does Rolled, a consideration of the chromosomal constitution of Pinched and Hedge was necessary. Pinched strongly resembles Sugarloaf, the secondary of Rolled, and less markedly Strawberry, the secondary of Buckling, and has, it is believed, in its extra chromosome the Strawberry half of the Buckling chromosome joined to the Sugarloaf half of the Rolled chromosome, justifying the chromosomal formula ($2n + 1/2St\ 1/2Sg$). A chromosomal diagram is given for Pinched, showing the probable method of disjunction leading to the formation of Buckling and Rolled egg cells and pollen grains.

Similarly, Hedge shows resemblances to Polycarpic, the secondary of Rolled (complementary to Sugarloaf), and also to Mutilated, the secondary of Echinus. It is the belief that it has in its extra chromosome the Mutilated half of the Echinus chromosome joined to the Polycarpic half of the Rolled chromosome, justifying the formula ($2n + 1/2Mt\ 1/2Py$).

Nubbin may be considered to be compounded of Pinched and Hedge, having as extras both the Pinched and the Hedge compound chromosomes (which together furnish the two opposite halves of the Rolled

chromosome), and lacking a single whole Rolled chromosome. Morphologically, therefore, Nubbin should show no Rolled characters, since it would possess the factors of only two Rolled chromosomes. Its chromosomal formula may be written $2n - 1 Rl + 1/2 St + 1/2 Sg + 1/2 Mt + 1/2 Py$. Chromosomal diagrams are given for Nubbin, indicating its probable constitution and the methods of disjunction that might lead to the formation of Normal, Nubbin, Pinched and Hedge gametes.

The paper presents a method of analysis as well as contributes to the solution of a special problem in *Datura*. Reference is made to investigations in progress as to the nature of "A" and "B" whites and of lines which when crossed together produce F_1 's with a definite proportion of aborted ovules and pollen grains. The belief is expressed that responsibility for the peculiarities of these races may be laid to chromosomal changes similar to those believed to have occurred in the production of Nubbin.

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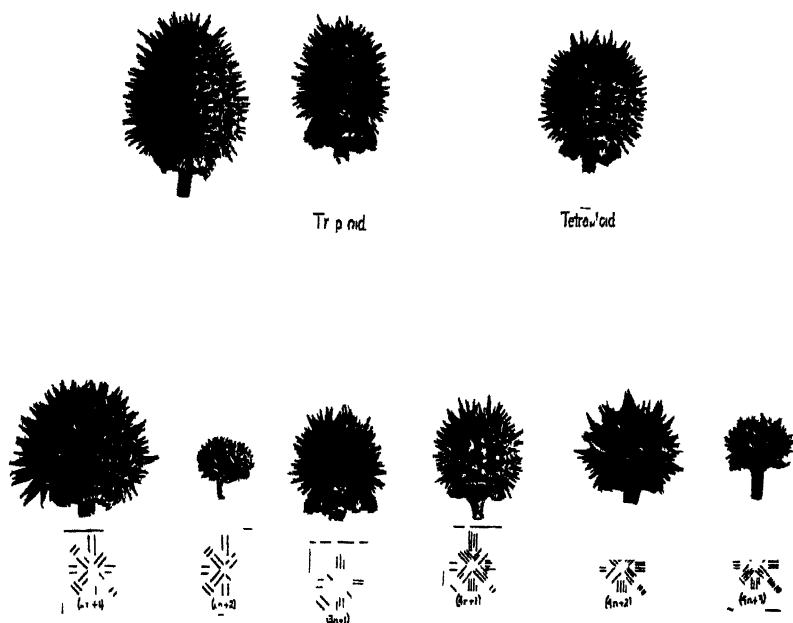
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CAPSULES OF SIX GLOBE MUTANTS

Normal diploid ($2n$), triploid ($3n$) and tetraploid ($4n$) capsules are shown above. Below, on the left, are two diploid Globes, with respectively one and two extra chromosomes in the Globe set. On the right there are three tetraploid Globes, with respectively one, two and three extra chromosomes in the Globe set. In the middle is a triploid Globe with a single extra chromosome in the Globe set. An increase in Globe peculiarities—depression of capsules and relative stoutness of spines—is seen as the number of extra chromosomes in the Globe set increases. [This figure is the same as (14, Fig. 6), with the addition of the triploid and the $(3n+1)$ Globe].



A



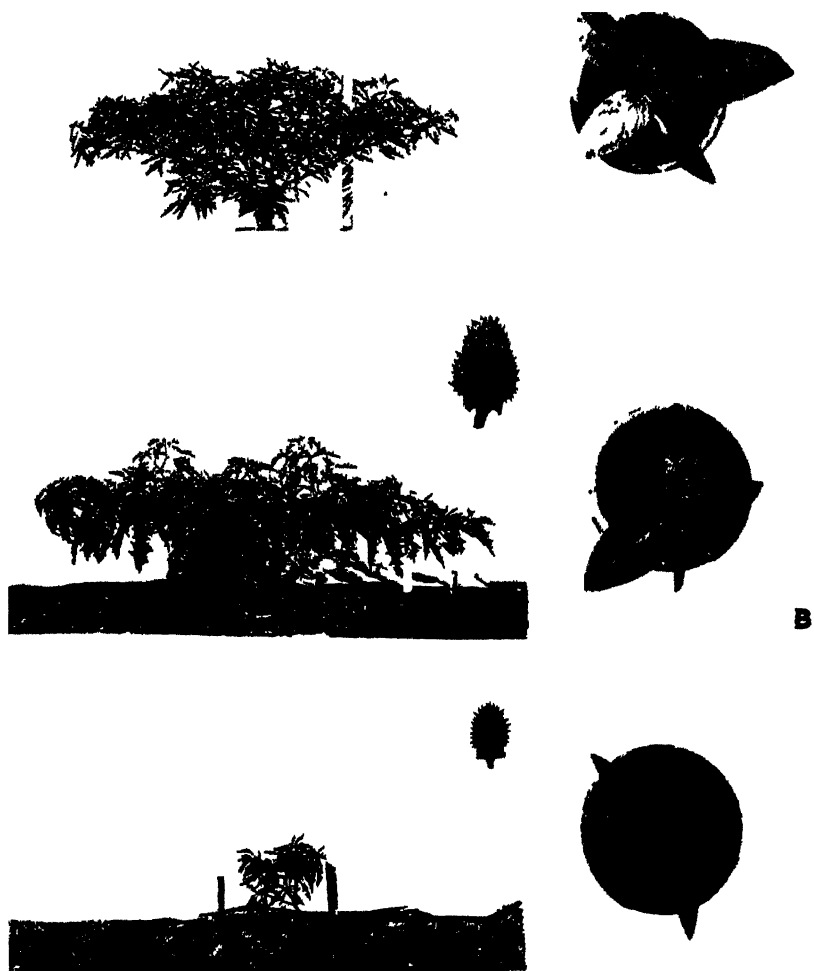
B



C

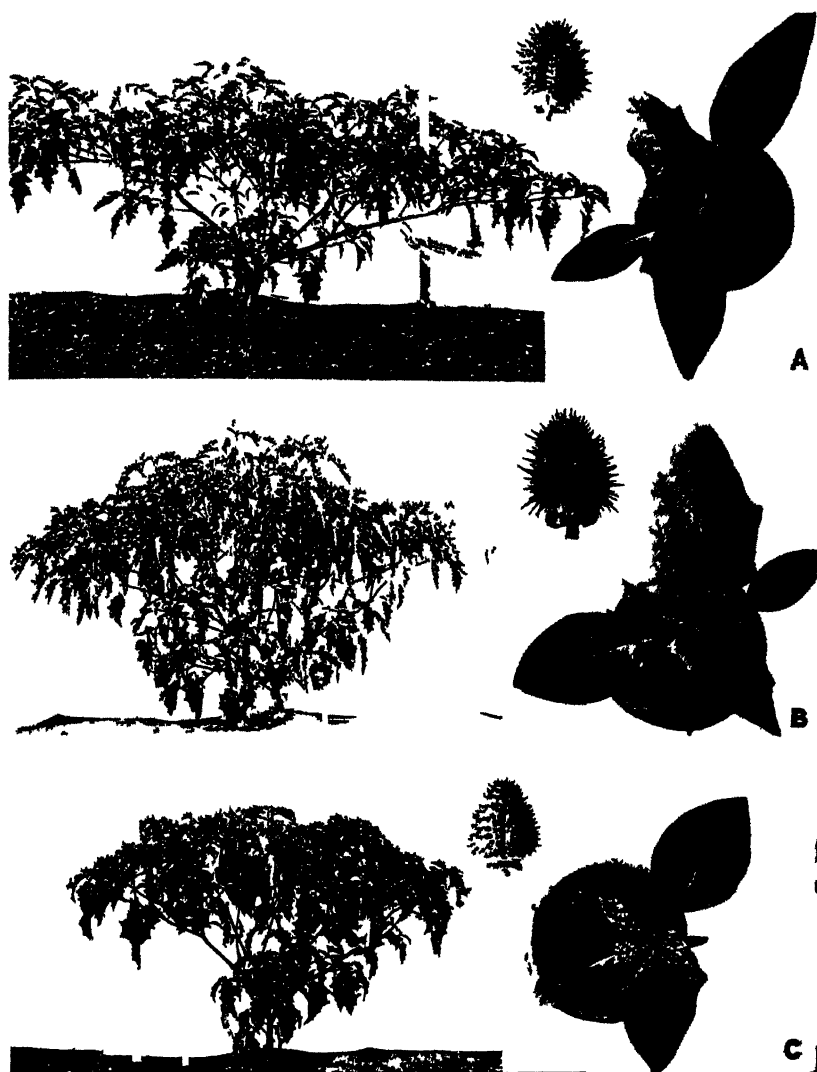
THE LUCKIN $(-n+1)$ GROUP

Showing garden habits, seedlings and capsules. A above the primary Fuchsia B in center one of its secondaries Strawberry C below the other complementary secondary Mistle



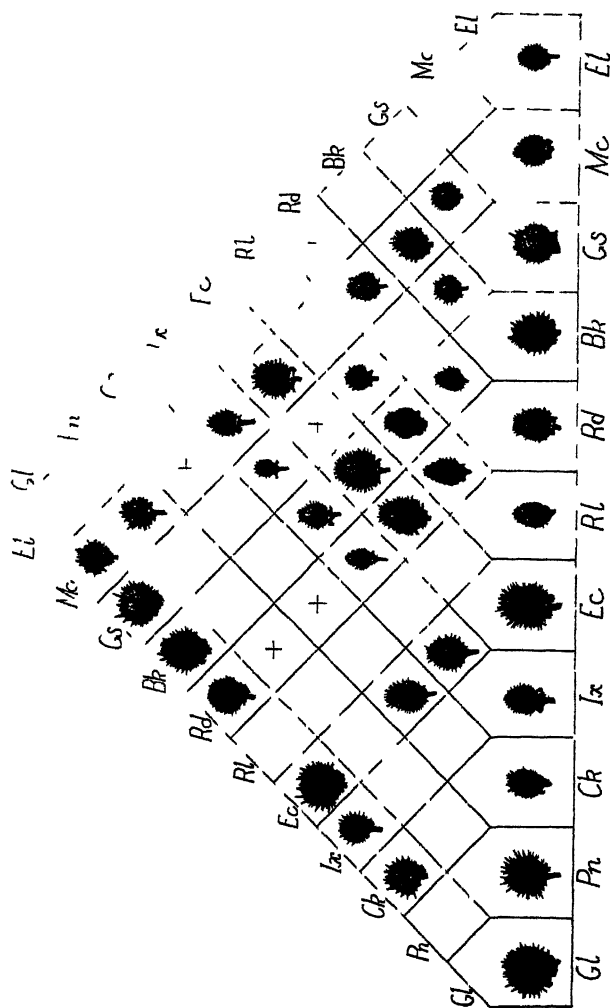
THIN ROLLED ($2n + 1$) GROUP

Showing garden habits, seedlings and capsules; A above, the Primary Rolled; B in center, one of its secondaries, Sugarloaf; C below, the other secondary, Polycarpic. For chromosomal diagrams of this group see Fig. 5. For photographs of the tops of capsules, see Plate VIII.



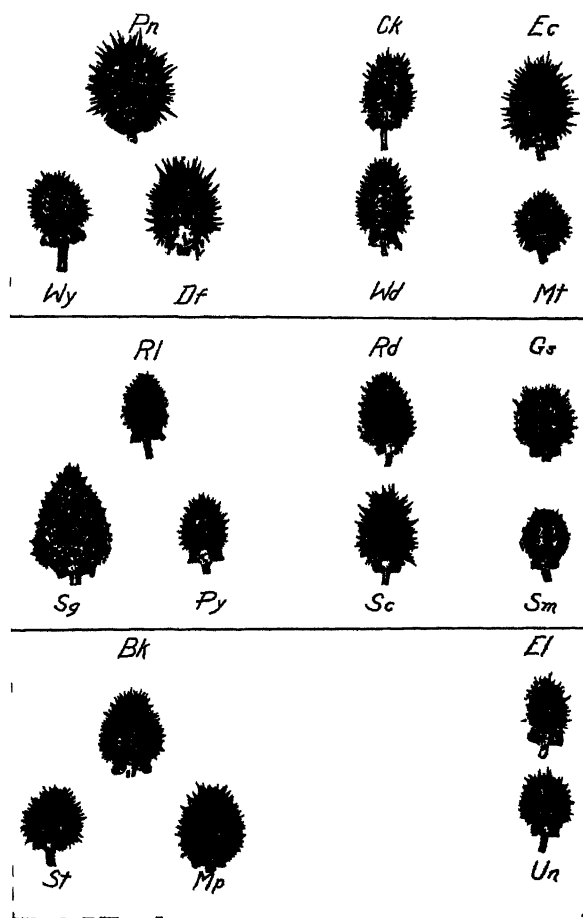
THE NORMAL DIPLOID ($2n$) AND THE ICHINUS ($2n+1$) GROUP

Showing garden habits, seedlings and capsules. A above the normal diploid. B in center the primary Ichinus. C below, its secondary Mutilated. The secondary of Ichinus complementary to Mutilated has not yet been found.

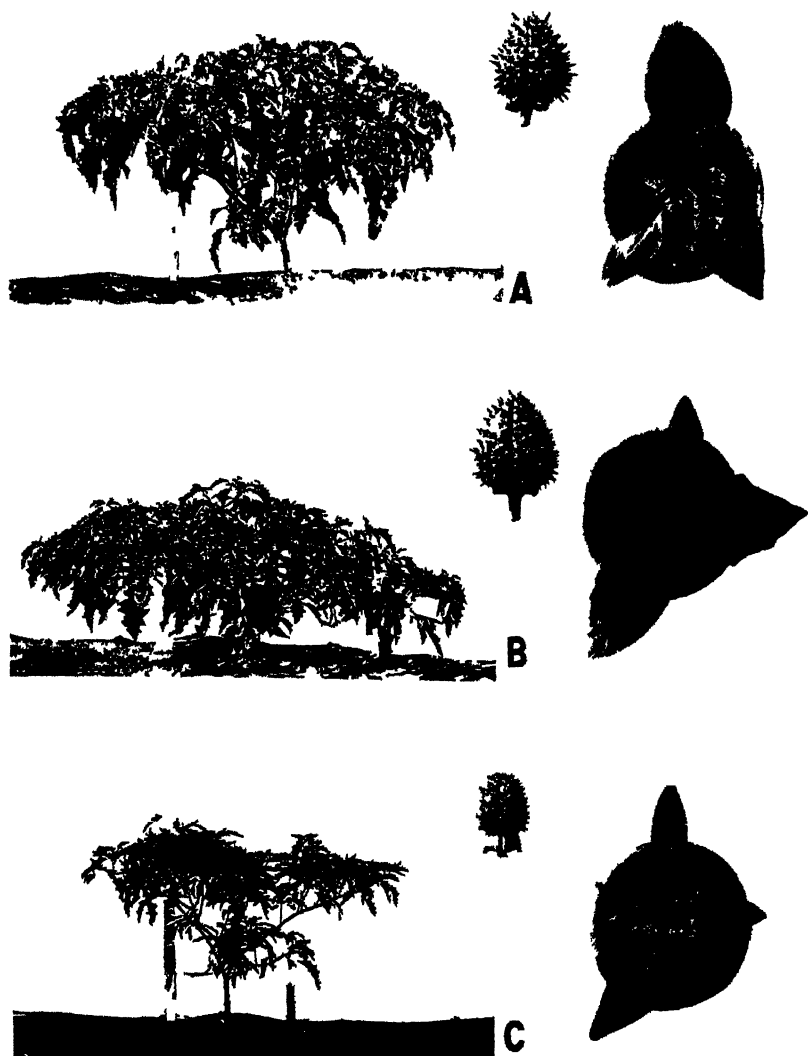


PRIMARY AND DOUBLE CHROMOSOMAL MUTANT TYPES IN THE OFFSPRING OF TRIPLOID (3n) PARENTS

Capsules from plants grown in the garden, 1925. Lower horizontal row contains capsules of eleven of the twelve theoretically possible primary ($2n+1$) types. Diagonal rows contain capsules of double ($2n+1+1$) types (cf. Fig. 1). Crosses (+) indicate plants identified for which no capsules were available. Each double type may be considered a combination between two primary ($2n+1$) types, since it has two extra chromosomes in different sets corresponding to the extra chromosomes in the two respective primaries listed at the ends of the intersecting column.

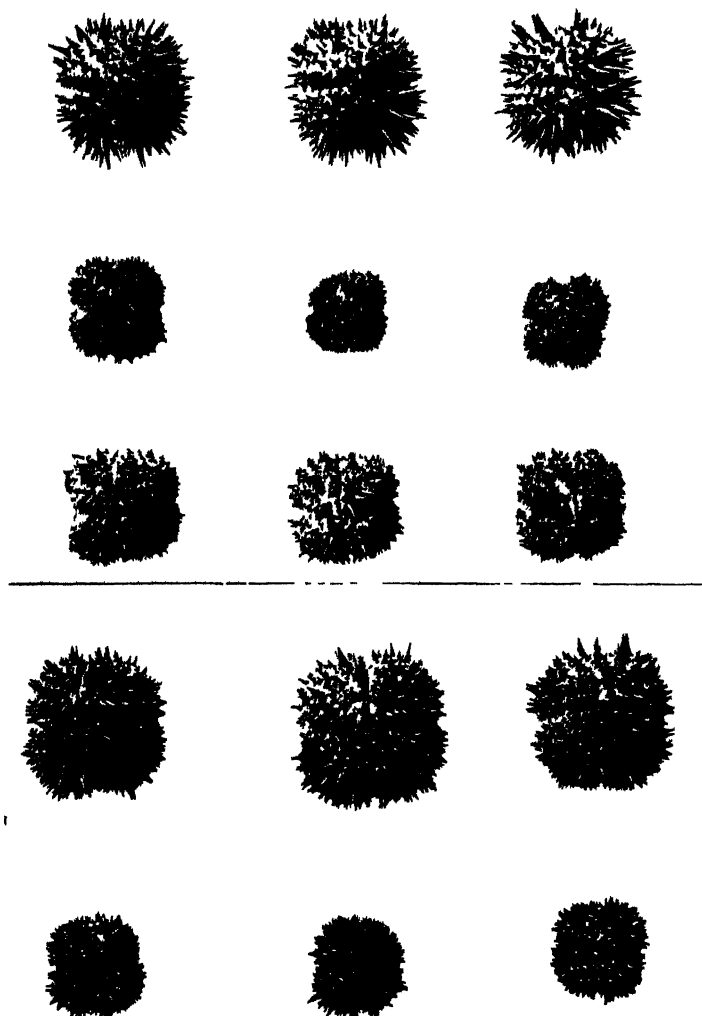
CAPSULES OF PRIMARY ($2n + 1$) TYPES AND THEIR RESPECTIVE ($2n + 2$) SECONDARIES

Above at the left, is *Polnsettia* (Pn) with its secondary, Dwarf (Df), and with *Wiry* (Wy), which has been shown to be a tertiary. Next is *Cocklebur* (Ck) with its secondary, *Wedge* (Wd), and at the right is *Echinus* (Ec) with its secondary, *Mutilated* (Mt). This capsule of *Mutilated* is deformed by a disease, as is often the case. In the middle row at the left is *Rolled* (Rl) with its two complementary secondaries, *Sugarloaf* (Sg) and *Polycarpic* (Py), next is *Reduced* (Rd) with its secondary, *Scalloped* (Sc), and at the right is *Glossy* (Gs) with its secondary, *Smooth* (Sm). In the bottom row at the left is *Buckling* (Bk) with its two secondaries, *Strawberry* (St) and *Maple* (Mp), and at the right *Elongate* (El) with its secondary, *Undulate* (Un).



THE NUBBIN GROUP

Showing garden habits, seedlings and capsules. A above Nubbin. B center Pinched. C below Hedge. For photographs of tops of capsules of Pinched and Hedge see Plate VIII. In Fig. 5 Pinched and Hedge are contrasted with Sunflower and Polycarpic the secondaries of Rolled. Chromosomal diagrams of Pinched and Hedge and Nubbin are given in Figs. 6, 7 and 8.



TOPS OF CAPSULES OF NORMAL DIPLOID (TOP ROW); ROLLED, SECOND ROW; SUGARLOAF, THIRD ROW; PINCHED, FOURTH ROW; HEDGE, BOTTOM ROW

Sugarloaf has thick overlapping spines at the apex. In the complementary secondary, Polycarpic (not shown in the photograph), these thick spines at the apex are lacking. In the primary, Rolled, the condition is intermediate between its two secondaries, Sugarloaf and Polycarpic. Pinched, it will be seen, resembles Sugarloaf in having thick apical spines while in Hedge as also in Polycarpic these spines are absent.

THE VALUE OF LIFE HISTORY DATA IN THE STUDY OF THE EVOLUTION OF THE AMPHIBIA *

By G. K. NOBLE

CONTENTS

	Page
Introduction.....	31
General statement.....	31
Breeding behavior as evidence of relationship.....	33
Acknowledgments.....	37
Caudata.....	37
Hynobiidæ.....	37
Cryptobranchidæ.....	41
Sirenidæ.....	42
Proteidæ.....	43
Ambystomidæ.....	44
Salamandridæ.....	46
Amphiumidæ.....	50
Plethodontidæ.....	51
Gymnophiona.....	59
General discussion.....	59
Salientia.....	60
Liopelmidæ.....	62
Discoglossidæ.....	69
Pipidæ.....	70
Pelobatidæ.....	74
Bufonidæ.....	81
Hylidæ.....	93
Brachycephalidæ.....	103
Ranidæ.....	105
Polypedatidæ.....	111
Brevicipitidæ.....	113
Discussion.....	117
Conclusions.....	119
Bibliography.....	120

INTRODUCTION

GENERAL STATEMENT

It is well known that many Amphibia do not undergo the ordinary development of *Rana* or *Ambystoma* but exhibit some "unusual mode"

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of life history. The eggs instead of being laid in the water are deposited on land, where the larvæ may either make their way back to the water with or without parental help, or they may hatch out of the egg-capsules as fully formed tetrapods. Frequently the parents build strange nests to protect the eggs and larvæ during their development. Naturally these remarkable life histories have excited the attention of biologists for many years, and from time to time convenient summaries of the published accounts have appeared.

From the summaries it would be gathered that the development of Amphibia is extremely plastic, two closely related forms frequently having totally different methods. Most reviewers—Boulenger (1886 and 1910), Brandes and Schoenichen (1901), Sampson (1900), Kerr (1919) and Barbour (1926)—have grouped those species which have somewhat similar methods regardless of the systematic relations of the species. A number of investigators have attempted to utilize different larval characters in a system of classification. Among the Salientia, the form of the larval teeth, the position of the vent and the spiracle were at one time considered of diagnostic value. As the larvæ of more forms became known, none of these characters was found to hold.

Within the last ten years life-history studies of the Amphibia have greatly increased, especially in southern Asia, tropical America and Australia. Numerous larvæ have been described and considerable data brought together which may be of use in identifying the species. Cannot some of these data be of value in showing the broader relationships of the forms considered? Should not life history give important clues to the evolution of the various groups? I have recently shown (1925) that much confusion concerning the importance of life-history work in phylogenetic studies has arisen in the past because of faulty assumptions as to the relationships of the groups. Recent advances in the elucidation of these relationships have removed many of these difficulties and it is now clear that the mode of life history often affords valuable evidence as to the phylogeny of a group (Noble, 1925).

In the expression "mode of life history" there are included two very different sets of phenomena: first, the breeding habits of the adults and, second, the development and larval habits of the offspring. In both fishes and birds it is well known that certain distinctive nesting habits may run through a family or a group of related genera. Familiar examples are found in the sticklebacks and the sunfishes (Centrarchidæ), the orioles and the horn bills. The weaver birds of the subfamily Ploceidæ construct one kind of nest, while those of the subfamily Estrildinæ con-

struct another. Sushkin (1923) has shown that our common English sparrow is not a typical sparrow at all but a weaver bird, as indicated not only by its anatomy, but also by its nest form. The nests of the primitive birds, such as the hawks, herons, pigeons, etc., are simpler than those of the passerine birds, but it would be difficult to trace a phylogeny of nest construction in any group of vertebrates. Habits, one would imagine, are easily changeable and hence not very "fundamental." On close scrutiny, however, habits in many of the lower vertebrates are found to be quite the contrary, for they owe their existence to the inherited organization of the form. They are instincts and may be more stable than many structural characters.

Only those characters can be considered fundamental which have been judged in conjunction with all that is known concerning the relationships of a group. The allantoic placenta is characteristic of the placental mammals, but it occurs again in certain, but not all, scincoid lizards. Sharks vary enormously in both placentation and in methods of fertilization. But in the urodeles external fertilization is found only in a single natural group of genera. Many apparently trivial habits may prove upon analysis to be more conservative and hence better indicators of relationship than the detailed features of development. The casual observations of a traveler in regard to the habits of an exotic amphibian may throw in some cases more light upon its relationships than a complete dissection of the adult. There is no way of knowing *a priori* whether habit, and by this I mean instinct, or structure is the more conservative in evolution.

Some habits, just as some specific characters, have arisen independently in different stocks. This is equally true of some breeding habits, such as the buccal brooding in the cichlid and silurid fishes. In the Amphibia certain habits crop out again and again in different stocks. In general the more specialized the habits or the more specialized the structures, the greater is the probability that they will occur only in closely related forms. In the following pages emphasis is laid on the most specialized habits and larval structures, as these are the most valuable in phylogenetic studies.

BREEDING BEHAVIOR AS EVIDENCE OF RELATIONSHIP

Before turning to a detailed discussion of the life histories, it may be pointed out that certain features of the breeding behavior have previously been used as evidence of relationship in the Amphibia. This is true of the courtship of salamanders. In the frogs and toads the males attract the females to them by their voices (Noble, 1923), and sex

recognition is accomplished by the differential action of the two sexes (Cummins, 1920), or possibly by some chemical sense (Banta, 1914). There is at least no courtship other than the calling, the differential movements and sounds when pairs come in contact and the embrace. In the salamanders the courtship is often very elaborate. As no attempt has previously been made to sketch an evolution of this ceremony throughout the order, it may be of some interest to see how far a progressive elaboration of the courtship behavior has gone hand in hand with the splitting up of the urodeles into natural groups.

In the most primitive urodeles, the Hynobiidæ, the courtship occurs in early spring. The males come first from hibernation and resort to temporary pools, slow-moving streams or more permanent bodies of water. They are followed a day or so later by the females. The sexes swim back and forth in the water, stimulating each other by these movements and also by quivering motions of their tails. Eggs are laid and the males swim over these, fertilizing them as they move (Dunn, 1923).

The Cryptobranchidæ, which are merely permanent hynobiid larvae of large size, are forced by their physiological requirements to breed in the streams in which they live. But during the breeding season a change in habits occurs. The animals become more social and gather in groups. They are apparently stimulated by one another's presence. Fertilization is external as in the Hynobiidæ. The presence of the string of eggs seems to be the immediate stimulus for the emission of a sperm cord by the male (Smith, 1907). To judge from the published descriptions, the same conditions obtain in the Hynobiidæ, where, however, the sperm apparently do not form a cord.

The ambystomids seem to have arisen directly from the hynobiids. It is interesting to note that the courtship of *Ambystoma maculatum* is very similar to that of the latter family. The males precede the females to the pond and gather together in groups. A *Liebesspiel* often takes place. C. M. Breder, Jr., and R. B. Breder and I have independently noted such a behavior at Millburn, N. J.; and later R. and L. Boulton and I at Syosset, New York. The sexes squirm actively about over and under one another. The males apparently do not distinguish other males from the females. The males rub each other with their snouts, the movement beginning anywhere on the lateral or under surfaces of the tail or body and proceeding forward. According to Wright and Allen (1909) the males later can distinguish between the sexes, and the rubbing movements directed against the sides and under surface of a female lead to

the deposition of a number of spermatophores. In one or more of these the female is sufficiently interested to approach until her cloaca is in contact with it. Fertilization is internal.

Within the genus *Ambystoma* further observation may show that there is some variation in the courtship. For example, the spermatophores of *A. jeffersonianum* are unknown and both Allen and Bishop have noted the males embracing the females. In the courtship of the axolotl the rubbing movements occur but, in addition, the male actively waves his tail. The latter movement will very likely be found throughout the genus, for it is probably associated with the spread of the secretion of the abdominal gland into the water. It has been noticed by European workers that the female axolotl takes a decided interest in the male and endeavors to bring her snout in contact with his cloaca. Chauvin noticed a similar behavior in the metamorphosed adult. The courtship of none of the other species in the family is known in sufficient detail to be discussed here.

In the Salamandridæ, which are not closely related to the Hynobiidæ but may have evolved from a pro-hynobiid stock, various types of courtship appear which seem to define natural groups of species even though these groups are not often distinguished by a generic or subgeneric name. The most primitive species, as represented by *Pleurodeles waltil*, have taken over some of the behavior pattern of *Ambystoma* and further elaborated it. The male creeps under the female and with his front legs grips her front legs from behind, thereupon swimming about thus for hours (Boulenger, 1910) with the female on his back. He then releases his hold and brings his cloaca over the female's nostrils. The female reciprocates with certain caressing movements of the head and finally the spermatophore is emitted. The courtship is very much the same in the closely related *P. hagenmulleri* and *P. poireti*, and possibly the embrace occurs in *Chioglossa* (Boulenger, 1910).

The peculiar embrace of *Pleurodeles waltil*, which I have seen in the laboratory, may be considered a salamandrid character. It is found not only in the species just mentioned, but also in the courtship of *Salamandra caucasica*, which takes place in the water, and in the courtships of *S. maculosa* and of *S. atra*, which occur on land. It is characteristic also of the primitive *Tylototriton verrucosus*. It seems to have arisen from the ambystomid habit of the male in rubbing his head on the under side of the female. Although it is found in no other family, it is not found throughout the Salamandridæ.

Most European newts are brightly colored, and the males "display"

before the female without embracing. In the American newt, *T. viridescens*, sexual dimorphism is less pronounced and the male makes very sure that the female is properly stimulated. He grips the female with the hind legs and forces a battery of hedonic glands against her nostrils. In the meantime his tail is vibrating rapidly and directing not only a current of water against the female but apparently also the contents of his abdominal gland. In the western newt, *T. torosus*, which is only distantly related to the eastern form, the male grasps the female with both pairs of legs as soon as they enter the water (Storer, 1925). Turning to the mountain newts of Europe, *Euproctus*, which form a very natural group, we find that the male grips the female with his hind legs and prehensile tail. The male of two of the species (*montanus* and *rusconi*) of this genus further maintains his hold by using his teeth. In all of the salamandrids the female is at first cold to the advances of the male. The different methods of courtship not only serve to excite the female but also to conserve the sperm, for in none of these forms is there a wasteful casting about of spermatophores as in *Ambystoma maculatum*.

The plethodontids have been directly evolved from the salamandrids. They arose from a mountain-brook stock, but none of them, so far as is known, practise a courtship similar to *Euproctus*. On the other hand, most of the species are provided with elongated premaxillary teeth and an enlarged mental gland (Noble, 1927). I have watched *Eurycea bislineata* in an aquarium at night and have noticed that the adults frequently rub their chins over each other. Mertens considered such a movement in *Hydromantes* as part of the courtship. Whether or not this is a correct interpretation, the fact remains that no other urodeles have the premaxillary teeth elongated as in the plethodontids, and it is not unlikely that a distinctive type of courtship will be found throughout this family.

Thus, in the urodeles certain types of courtship characterize different groups. Distinctive behavior patterns are not always found in all members of any one group. Nevertheless, these behavior patterns when they do occur are diagnostic of an animal's relationships. Behavior characters are not always so clear-cut as morphological ones but, as instinctive habits are based on an animal's inherited morphological as well as physiological organization, one may feel hopeful of tracing the main evolutionary changes in these habits in the same way, even if not with the same exactness, that one traces out the phylogenetic changes in the skull.

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CAUDATA

HYNOBIIDÆ

The Hynobiidæ embrace a group of *Ambystoma*-like salamanders found only in Asia. The many differences which separate these salamanders from the ambystomids have been pointed out by Cope (1859, 1889), Druner (1904), Dunn (1922, 1923), and others. They are the most primitive of living salamanders and are possibly directly ancestral to the ambystomids.

In this family there is a remarkable uniformity of life history. Dunn (1923 a) has published a splendid review of the group, giving translations of many obscure papers dealing with the life histories. Fertilization is external. The eggs are always laid in two sacks (apparently the unfused contents of each oviduct) which have a peculiar spindle-like shape. *Hynobius*, the least specialized genus of the family, has a life history very similar to that of *Ambystoma maculatum*. The eggs vary in size from 2.5 to 3.2 mm. (exclusive of capsules). There are from thirty-five to seventy eggs within each egg-sack. The eggs are laid in ponds, temporary pools, springs or even shallow, slow-moving streams. One end of the egg-sack is usually attached, although rarely the sacks are found free on the bottom. The early larvæ, so far as known, are all *Ambystoma*-like with a dorsal fin, balancers and long external gills. The legs develop slowly, the anterior pair in advance of the posterior ones. In short, there is nothing in the life history of *Hynobius*, except the external fertilization and the spindle shape of the egg-sacks, to distinguish it from that of the pond-breeding species of *Ambystoma*. A close comparison will show minute differences. The double balancers of *H. naevius*, for example, have been found only once in *Ambystoma*, but on the whole the details are astonishingly similar.

Dunn (1923 a) recognizes four genera of hynobiids in addition to *Hynobius*. These four are all mountain types apparently derived from *Hynobius* directly. The life histories of only two of these genera are known. These two have assumed different types of adaptation the one from the other.

Onychodactylus frequents the edges of mountain torrents. In the case of salamanders which have taken up a more or less permanent abode in this habitat the lungs invariably have been lost or greatly reduced. Among the Ambystomidae, we find that this is the case with *Rhyacotriton*; among the Salamandridae, no less than seven species are thus modified, as pointed out by Boulenger (1917). All the more primitive plethodontids occupy this "niche in the environment," which, because of its humidity and coolness, must have a very high oxygen content, permitting skin respiration alone (with aërial bucco-pharyngeal respiration) to suffice the needs of these salamanders (Noble, 1925 a).

Ranodon, although found usually at higher altitudes than *Onychodactylus*, has invaded a different habitat. Instead of frequenting the dripping banks of the streams, it hides away under the rocks in the water, coming out only when searching for food. In this habitat the lungs are retained, apparently serving for respiration. It would seem that any hydrostatic function would be out of place in these mountain torrents (compare Annandale and Hora, 1922).

Structurally neither *Onychodactylus* nor *Ranodon* are very different from *Hynobius*. Their life histories are also similar. *Ranodon* retains the spindle-shaped egg-sacks while the eggs of *Onychodactylus* are unknown. *Onychodactylus* apparently breeds in situations similar to those of *Hynobius* but the water selected is sometimes colder and swifter. The egg-sacks of *Ranodon* are fastened to the under side of flat stones beneath which the water flows. The eggs are larger than those of *Hynobius* and fewer in number. Schmalhausen (1917) gives the diameter of a fixed egg (without capsules) as 4 mm. The larvæ hatch in a more mature condition than those of *Hynobius*. Schmalhausen makes it clear that the broad dorsal fin and elongated larval toes of *Hynobius* are lacking. According to Snitnikov, quoted by Dunn (1923), there must be some indication of a dorsal fin.

The larvæ of *Onychodactylus* have the fin restricted to the tail, and are shod with horny pointed nails (Fig. 1). They differ remarkably from the larvæ of all other Amphibia in having a fin on the outer edge of both fore and hind limbs.

How many of these life-history details can be considered evidence of close relationships, and how many are characteristic of all urodeles

occupying similar habitats? We may glance ahead a little to the mountain-brook breeders of other families and note certain features which tend to reappear in all:

1. Loss of dorsal fin of the body and its restriction to the tail.
2. Reduction of gill rachis, the gill filaments appearing short and bushy, not branch-like.
3. Loss of balancer.
4. Increase in size of egg and reduction in the number of eggs.
5. Nearly simultaneous appearance of the digits, or at least no great exaggeration of the preaxial ones.

These characters are not modifications called forth in each ontogeny by the environment. If the larvæ of the two-lined salamander is raised in quiet water, it does not develop the larval peculiarities of the spotted salamander (*Ambystoma maculatum*). Not all of the characters, however, are known to occur in the mountain-brook hynobiids, for the larvæ



FIG. 1.—Larva of *Onychodactylus japonicus* showing the peculiar fins on the legs and the recurved claws on the digit tips.

of these forms are only incompletely recorded. Further, there is at least one recent invader of the stream habitat, *Ambystoma altamirani*, which has not acquired all the characters. In this species the dorsal body-fin is reduced but not absent. On the other hand, a few pond-breeders may occasionally exhibit certain of the features. *Ambystoma tigrinum* normally lacks the balancer, and the bottom-dwelling larvæ of the Sirenidae and Proteidae have no dorsal fin. Undoubtedly, the first three features are of value to any larvæ living in swift water and lying close to the bottom, as these forms do. Such characters may have been fixed in these forms by natural selection. The last two characters do not seem to be of any advantage to a swift-water dweller and therefore require further explanation.

The eggs of most stream-breeding and terrestrial Amphibia are larger than those of pond-breeders. Does this mean that the latter are more primitive? There is no evidence as to the size of the eggs that the immediate ancestors of the modern Amphibia may have had, although various hypotheses have been advanced (de Bussy, 1905; Mehely, 1901; Boulenger, 1910; Dunn, 1923). Egg size may vary enormously within

a genus such as *Rana* and, if we trace through the phylogeny of certain families, such as the Hylidæ, there will appear certain obvious cases of secondary loss of yolk. In the Hynobiidæ the smallest eggs are found in the most primitive genus, *Hynobius*. But this may be merely a consequence of life in the pond. Certain families of Amphibia exhibit a fair constancy in egg size, but others vary so greatly that the actual egg size of the ancestors of the modern forms has apparently had no effect on the evolution of the group.

The small egg size of *Hynobius* is, nevertheless, responsible for certain larval peculiarities which appear in this genus and also in our common pond-breeding newts and *Ambystoma*. There is a disproportionate growth of the preaxial digits. The postaxial digits, especially of the forelimb, seem to sprout from the sides of the former. This led to the hypothesis advocated even today by some authors, that the primitive chiropterygium arose by budding from the side of a primitive ray. As discussed elsewhere (Noble in MS.), this is far from likely. The problem of the significance of this disproportionate growth has been attacked experimentally by Schmalhausen (1925), who starved larvæ of *Triturus cristatus* which were developing their digits. Starvation tended to accentuate the disharmonic growth. Further, if the limb was cut off in an early larva, it regenerated asymmetrically, while in older larvæ all the digits tended to appear at the same time. Schmalhausen interprets this difference as due to nutrition. All the digit *Anlagen* would have the same chance of getting started in their growth in well nourished limbs, while in the poorly nourished appendages, only the preaxial *Anlagen* the first to get started, can initiate growth. The amount of nutriment would seem to control the number of *Anlagen* which can develop at one time. The histogenetic processes, on the other hand, are not controlled by the amount of nutriment available and the first digits to appear rapidly differentiate into functional fingers. Thus the ancestral Amphibia, if they were poor in yolk, possessed an early disharmonic growth of the digits; if they were well provided with yolk, all the digits appeared at about the same time. The same condition obtains today in the Crustacea: those with small eggs show an early histogenesis of a few appendages, those with large eggs have the limbs developing at about the same time.

In the present state of our knowledge, the only distinctive features in the life history of the Hynobiidæ as a family are the spindle-like egg-sacks. Probably when the larvæ become better known, other characters will appear. In no other family of Amphibia are the egg-capsules distinctive of the whole group. This does not preclude our recognizing

the egg-sacks of the Hynobiidæ as an important family character. True toads (*Bufo*) all over the world (except a certain dwarf species) lay their eggs in characteristic strings. In the Hynobiidæ the egg-capsule form is characteristic not of a genus but of a whole family. Thus, changes in skeleton organization have evolved much faster in this family than changes in those oviducal and cloacal structures which control the form of the egg mass.

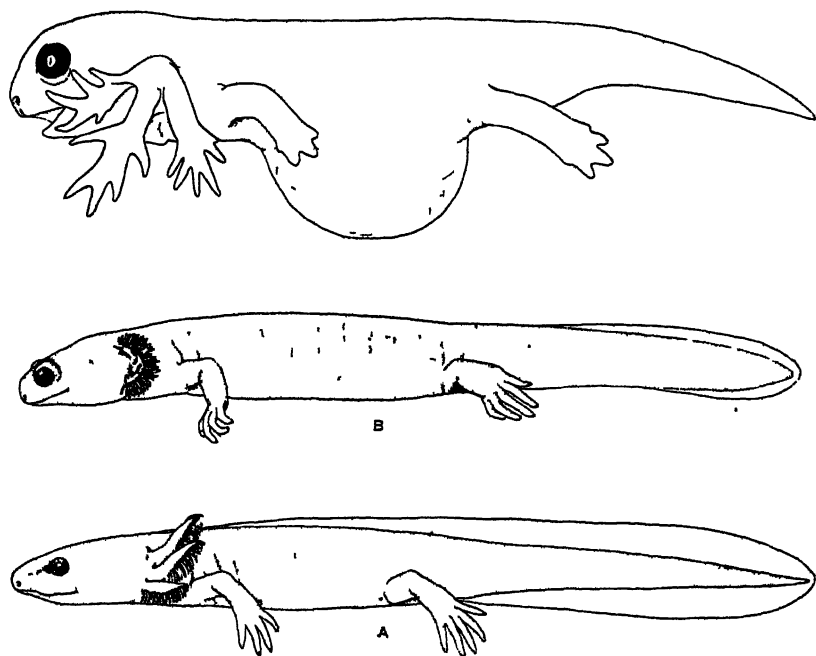


FIG. 2—The principal types of urodele larvæ: (A) pond type, *Ambystoma parotum*; (B) mountain-brook type, *Dicamptodon ensatus*; (C) terrestrial type, *Plethodon randykei*.

CRYPTOBRANCHIDÆ

The two genera which comprise this family are both "permanent larvæ" of some unknown hynobiid. *Cryptobranchus* in its open branchial clefts and greater number of branchial arches is more larval, and has assumed fewer metamorphic changes than *Megalobatrachus*. The life history of these two genera, as shown by Smith (1912) and others, is practically identical. Their life history does not differ radically from that of *Ranodon sibiricus*. Fertilization is external. The "slim and spindle-shaped" egg-sacks of the latter species are here elongated until they form two cords. The outer egg-capsule does not form a sack but

merely a covering to the individual eggs and the gelatinous connection between eggs. The eggs, although large, are proportionately smaller (as compared with body length of female) than in *Ranodon*. They are also more numerous. A detailed comparison of the egg-capsule and larvæ cannot be made because of our inadequate knowledge of the development of *Ranodon*. It should be noted, however, that *Cryptobranchius* larvæ have no body fin, no elongate digits at an early stage and that their external gills are short. Most of these "swift-water adaptations" are found in the larva of *Onychodactylus* (Fig. 1).

SIRENIDÆ

Siren and its small relative, *Pseudobranchius*, are the "most larval" of all salamanders. Their relationships are unknown. Their osteological structure is that of an early ambystomid or salamandrid larva masked by the development of a series of unique specializations and by the acquisition of a few adult structures. The horny mouth parts of both larva and adult may be compared with the premental sheath of the larvæ of *Ambystoma* and of *Onychodactylus*. We might with Wilder consider the Sirenidæ a degenerate type and look for the life history as shedding some light upon their relationships.

Years ago when much greater consideration was given to ontogeny as affording a clue to solving problems of relationship, Cope thought he found in the ontogeny of *Siren* a feature which gave some proof of this group's antecedents. In a paper entitled "The Retrograde Metamorphosis of *Siren*" he concludes: ". . . the present Sirens are descendants of a terrestrial type of Batrachia which passed through a metamorphosis like other members of their class, but that more recently they have adopted a permanent aquatic life, and have resumed their branchiae by reversion."

I have recently shown (Noble, 1924 b) that gill reduction in *Siren* and *Pseudobranchius* is in no sense a metamorphosis but merely due to adverse conditions. Both of these genera normally possess well developed gills throughout life. If their aquatic habitat is dried up, the functionless gills undergo a rapid dwindling. *Pseudobranchius* and possibly *Siren* lay small eggs singly or in small bunches in ponds, according to Mr. A. S. Alexander, who sent me specimens of the former a few days after hatching. The recently hatched *Pseudobranchius* closely resembles the adult except that its anterior appendages are represented merely by limb buds. The larva, therefore, is very distinctive and approaches no other type (Fig. 3). The small eggs of *Siren* and *Pseudobranchius* may

be correlated with their pond habitat but the larva itself is radically different from the early larvæ of hynobiids, ambystomids or salamandrids. This would suggest that the Sirenidæ have no close affinity to these families.

PROTEIDÆ

The two genera of this family, *Proteus* and *Necturus*, are "more larval" than *Cryptobranchus* and "more adult" than *Siren*. They occupy an isolated position among urodeles, as has been pointed out many times. It is generally agreed (Kingsbury, 1895; Dunn, 1922; Dolivo-Dobrovolsky, 1923, etc.) that they are not closely allied to any existing family. We might expect from what we have seen in the preceding family, that their life history would not agree in detail with that of any other urodele and that these two genera would not differ from each other essentially. This is exactly what we find to hold true.

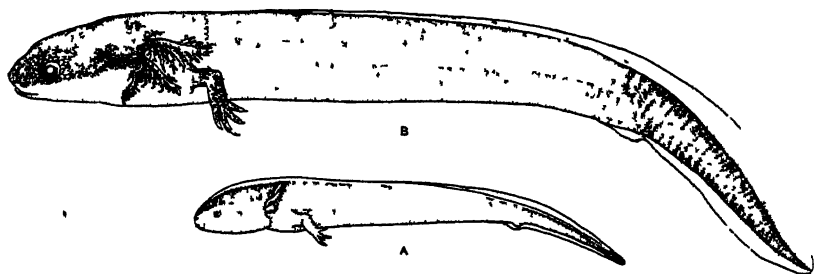


FIG. 3.—Sirenid larvæ: (A) *Pseudobranchius striatus*, 18 mm. total length; (B) *Siren lacertina*, 40 mm. total length. Note the great resemblance to the adult.

In both *Necturus* and *Proteus* the eggs are laid singly, attached to the under surface of a rock, board or other convenient object. The eggs of both may be laid in still water. Smith (1911a) has found the eggs of *Necturus* also in streams. The number of eggs varies in both genera. Smith records sixty-six as an average for *Necturus*, and fifty may be taken as an average for *Proteus*. Two well defined capsules surround each egg, Schulze (1876), Chauvin (1883), Zeller (1889). Smith (1912) has demonstrated the presence in *Necturus* of a double vitelline membrane in addition to the capsules. Each egg is attached to the covering object by means of its outer capsules. The eggs of both genera are large, 4 mm. being an average diameter for *Proteus*, while Smith (1911a) records the egg of *Necturus* as 5.8 mm. in diameter. It should be noted in this connection that *Necturus* is a larger animal than *Proteus* and the relative sizes of the two eggs would not differ greatly. The egg-capsules of *Necturus* are narrower than those of *Proteus*, but the form is the same.

There is a striking resemblance between the early larvæ of *Necturus* and *Proteus*. Both have the same shape of head and gills. Their appendages exhibit the same proportions. In short, the resemblances between the eggs and larvæ of *Necturus* and those of *Proteus* are very close.

Proteus occasionally exhibits one peculiarity of development which at first sight would seem to vitiate the conclusions reached from a comparison of the eggs and larvæ of *Proteus* with those of *Necturus*. Under certain abnormal conditions (Nusbaum, 1907), or even under more normal ones (Kammerer, 1901), *Proteus* may give birth to its young alive. No modifications of larval gills or of parental oviduct have been recorded. The small size of the eggs would make it necessary for *Proteus* to feed at an early stage. It is not improbable that the young *Proteus* feeds on the other eggs retained in the oviducts, but of this we have no information. In short, the *Necturus*-like eggs of *Proteus*, if retained within the oviduct, degenerate except for one (Nusbaum), or two (Kammerer), which develop apparently at the expense of the degenerating eggs but without especial modification of their own structure or of the oviduct in which they rest. Before it can be decided just how this is accomplished, further study is needed. It is important to note that the larvæ in this restricted environment are not known to be modified but agree with those of *Necturus*.

AMBYSTOMIDÆ

The ambystomids form a familiar group of North American urodeles. Dunn (1922) believes they have had a separate origin. It does not seem to me, however, that the fusion of angular and prearticular, the fracture of the hyoid, the reduction of the second epibranchial to the barest rudiment, the formation of an otoglossal and, finally, the increase in length of the premaxillary spines are differences so fundamental that such ambystomids as *Dicamptodon* or *Rhyacotriton* could not have evolved directly from the hynobiids. The cloacal differences afford a further objection but the uniform glandular condition of the hynobiid cloaca may possibly be a degenerate one. At least, we may conclude that the ambystomids are much more closely allied to the hynobiids than are the salamandrids.

The Ambystomidæ comprise two groups of genera which may have arisen from different hynobiid stocks. *Rhyacotriton* and *Dicamptodon*, as pointed out by Dunn, are closely allied and differ from *Ambystoma* in certain skull features. The egg-masses of all ambystomids differ from those of the hynobiids in form. They are not spindle-like and are

laid in one, or usually several masses. Internal fertilization is accomplished by means of spermatophores, which may be considered fragments of the sperm cord of *Cryptobranchus* attached to a mucilagenous basis (the product of the cloacal glands).

The eggs of *Dicamptodon* are laid in small mountain lakes of the California coasts. The egg-masses resemble those of *Ambystoma maculatum* except that, according to Storer (1925), there is only one capsule around each egg. Storer notes, however, that the inner lining of the egg-capsule may be removed in one piece. It is, therefore, possible that a second capsule is present, although very thin. The larvæ after hatching make their way to the mountain streams, for many have been captured in the latter habitat.

The eggs of *Rhyacotriton* are unknown, but ovarian eggs are large and few. The larvæ of *Rhyacotriton* live in the streams side by side with the *Dicamptodon* larvæ. Both are very similar and resemble the *Onychodactylus* larvæ, save for the limb fringes and the more sharply pointed horny tips to the digits of the latter. It is here that both environmental and hereditary factors are tending to produce similar forms. Both are genetic factors, for *Dicamptodon* larvæ kept in aquaria show no tendency to develop the pond-larval characters of *Ambystoma*.

The second group of ambystomids are all referred to the single genus *Ambystoma*. The larvæ are all of the pond type (Fig. 2). They agree with the larvæ of *Hynobius* in their broad tail and dorsal fin, their balancers (rarely absent), their elongated gills, each provided with a central rachis and many pairs of filaments. There is considerable variation of egg-capsule form and in the number of eggs laid. In some cases, *A. tigrinum*, *A. maculatum*, etc., the outer capsule encloses a number of eggs in a sack, which recalls the egg-sacks of *Hynobius*. In other cases, *A. jeffersonianum* (Smith, 1911), the outer capsule may be much thinner or, again, the eggs may be laid singly or in small bunches (*A. microstomum* and a western race of *A. tigrinum*). Two species, *A. annulatum* and *A. opacum*, lay their eggs on land but the larvæ, which soon get into water (thanks to the rains, in most cases), are of the usual type, having all the characteristics just described. Specific differences in the exact form of the gill filaments, the color of the larvæ, the rate of development and the shape of the egg-capsules may be recognized in these different species. The interrelations of these forms are not sufficiently well known to attempt any further correlation between larval habitus and relationships. It may be noted, however, that the two more terrestrial species, *A. opacum* and *A. annulatum*, are not closely related but have sprung

from different stocks. Further, *A. maculatum* on rare occasions lays its eggs on land (Smith, 1911; Brimley, 1920). Here, then, within a single genus we have two different groups tending toward land life and yet neither succeeding in freeing itself from the larval life and larval form of the genus.

There is one larval character of *Ambystoma* that deserves especial mention as it may, on further investigation, show a definite relation between the hynobiids and ambystomids—a relation already suggested by the structure of the adults. Long ago Carrière (1884) described in the axolotl a horny beak on the dentary anterior to the teeth. This peculiar structure, so suggestive of the larval mandibles of frog tadpoles, is found elsewhere among salamanders only in the hynobiid, *Onychodactylus fischeri*. Further search for this feature may establish its presence in other hynobiids and ambystomids. So far as we know it does not occur in any salamandrid.

SALAMANDRIDÆ

The Salamandridæ are related to both hynobiids and ambystomids, but probably arose from some pre-hynobiid stock, for they do not show close affinity to any existing genus of these two families. The family is a very difficult one to treat in the present connection, for the generic limits are not well defined nor are the relations of one genus to another in many cases known. A better appreciation of these difficulties may be had after a perusal of the discussion of the family given by Dunn (1918).

The most primitive genera are apparently those with a pronounced temporal arch and a maxillary extending back to the quadrate region (or nearly to it). This would include the genera *Tylostotriton*, *Pleurodeles* and some species of *Triturus*. As if in direct support of this anatomical evidence, these genera approach more closely to *Ambystoma* and *Hynobius* in their life history than do any other salamandrids. The eggs of *Tylostotriton* and *Pleurodeles* are essentially like those of *Ambystoma maculatum* (Boulenger, 1920). They are laid in ponds and the larvæ which emerge from them are of the "pond type": that is, they have the broad tail, dorsal fin and long gills already described under *Ambystoma*. *Triturus torosus*, the most primitive American salamandrid, according to Ritter (1897) and Storer (1925), usually lays its eggs in small bunches, which approach the condition in *Ambystoma*. The other newts were apparently derived directly from this primitive stock, which was, it would seem, widely spread in Asia. The derived forms are also a pond type but they lay their eggs attached usually singly to water weed. We

shall see in the Amphibia many species which lay their eggs singly, and most of these, it will be found, are derived from types which lay their eggs in bunches. *T. torosus*, itself, may on rare occasions lay its eggs singly instead of in bunches, just as *Ambystoma tigrinum* in the West is said to do. The larvæ of *Triturus*, *Pleurodeles* and *Tylototriton* are very similar, whether this be attributed to genetic relationship or to the similar mode of living (by natural selection).

As in the Hynobiidæ and Ambystomidæ, so here in the Salamandridæ we find types adapted to mountain life. These types universally exhibit a reduction in the lungs unless, as in the case of *Ranodon* and *Megalobatrachus*, they remain in the mountain streams. They also exhibit integumentary modifications to assist them in cutaneous respiration, as I have shown elsewhere (Noble, 1925). The mountain-brook larvæ of all three families, just like the adults, bear the definite stamp of their environment. Their gills are short, the body-fin is reduced or absent and the tail is narrow. *Chioglossa* and *Euproctus* are undoubtedly derived from different salamandrid stocks, but their larvæ are similar, at least in the characteristics just mentioned. This parallelism is unquestionably correlated with their mountain-brook habitat. A comparison between Despax's figure (1923, Fig. 44) of the larva of *Euproctus asper* and mine (Fig. 2 B) of the ambystomid *Dicamptodon* will show a startling resemblance due in no way to a genetic relationship but merely to their common type of habitat.

The eggs of *Chioglossa* are unknown but those of *Euproctus* have been described by Bedriaga (1895), Wolterstorff (1903) and more recently by Despax (1923). The eggs of *E. asper* are attached singly to the under side of stones in running water. They are pigmentless and of large size (4.5–5 mm.). The eggs of *E. rusconii* have been laid in the laboratory. They are practically identical with those of *E. asper* and strikingly different from the small eggs of *Triturus*. Despax (1923, p. 169) raises the query whether this large egg-size can be due to the cold water in which the eggs are laid, and he draws a comparison between the egg-size in certain cold- and warm-water fish. Large eggs are not universally characteristic of cold waters either in fish or in Amphibia. Egg-size is not like larval form—definitely correlated with a particular environment. It would seem, therefore, that similar egg-size in the two species of *Euproctus* is evidence of their relationship. Egg-size, at best, is not a good character, for in other groups it exhibits extreme variability.

Salamandrina includes only a single species, which has apparently

been derived directly from some of the more primitive newts, *Triturus*. Many other groups of urodeles parallel *Salamandrina* in the loss of a digit and the lungs. In some of these other families (Plethodontidæ, Hynobiidæ) the former character is frequently not considered of generic value. *Salamandrina*, although terrestrial throughout most of the year, furnishes, when the breeding season arrives, apparent proof of its immediate ancestry, for it seeks small protected pools in the mountain streams, where it attaches its eggs singly or in small groups to water weed or debris. The larvæ which develop are very similar to those of *Triturus* (Schreiber, 1912, p. 34).

In this connection the life history of our common eastern newt may be mentioned as there seems to be some misunderstanding in regard to it. *T. viridescens* has been described as differing from other members of the genus *Triturus* in that it has a long juvenile life on land, during which it assumes a radically different coloration from that which it exhibits either before or after. I have recently shown (Noble, 1926 d) that the red eft stage is not characteristic of all individuals of the species: those that live on Long Island and apparently in other non-mountainous regions skip over this stage, which may be considered a purely local modification produced during each ontogeny by the environment.

There remains to be discussed in this family only one genus, *Salamandra*, but, as this one has assumed the greatest larval specializations within the family, it is of especial interest to us. The thesis which we have been trying to establish is that elaborate embryonic or larval specialization would not occur twice in exactly the same way unless there were community of origin in the forms exhibiting these homologous specializations.

The affinities of *Salamandra* are not very clear, but such features as the long ypsiloid apparatus would indicate that it has been derived from the primitive *Pleurodeles*—*Tylototriton* stock alluded to above. Some authors, such as Cope (1889) and Dunn (1926 b), place *Salomandra* and the newts in different families. The evidence for this arrangement has not been published in full. The eggs of *Salomandra* are large and the larvæ are retained within the parent's body during a large part or during all of the larval period. *Salamandra* is a mountain form and the large eggs would at first sight suggest affinity to *Euproctus*. But the larva as it develops shows definite evidence of a "pond type" ancestry. A balancer is present in both *S. atra* and *S. maculosa*, although, of course, rudimentary and non-functional (Wunderer, 1910). This bal-

ancer we have found characteristic of all "pond type" larvæ, whether of *Hynobius*, *Ambystoma* or *Triturus*, and it is never found in any mountain-brook forms or in genera such as *Hemidactylus* which have been derived from terrestrial or mountain-brook groups. The adult *Salamandra* shows no mountain-brook adaptations, such as lunglessness, modified integument, etc. Both anatomical and larval data point toward a "pond type" ancestry for *Salamandra*.

Within the genus *Salamandra* we find what appears to be a considerable difference in life history. *Salamandra atra* gives birth to metamorphosed young, while *S. maculosa* produces larvæ in various stages of development. Wunderer (1910), impressed by the differences in egg size between these two species and their consequent differences in development, is inclined to believe the two species not closely related. We shall see later what enormous differences in life history may be occasioned by differences in egg-size. But if the species are closely related, we shall find that any extreme larval specializations tend to reoccur in the related forms. In *Salamandra* there are two conspicuous specializations: the highly vasculated oviducts of the adult and the long gills of the larva. The detailed structure of the oviducts was incorrectly described for *S. atra* by Wiedersheim (1890) and for *S. maculosa* by Stüve (1889). However, Schwalbe (1897) made it clear that there was no breaking down of the capillaries of the oviduct as Wiedersheim described. More recently Hirzel (1909), and especially Kaufman (1913), have added important details to these accounts. I have examined four "pregnant" female specimens of *S. maculosa* which had been kept so long away from water that a large percentage of the larvæ had escaped from the egg-capsules and were resting with their gills closely adpressed against the highly vasculated surfaces of the oviduct. The larvæ were undoubtedly receiving their oxygen supply and possibly some liquid nutriment from the maternal tissues. Their gills were long, although not so long as in *S. atra*. Whether the larvæ remain within the egg-capsules and are expelled into the water as is customary in *S. maculosa* or break out from the capsules and remain for a longer or shorter period within the oviducts is purely a time relation dependent on unsuitable environmental conditions, especially cold. It must be agreed with Schwalbe (1897, p. 392) that *S. atra* and *S. maculosa* have essentially the same parental and larval modifications.

In order to reply more definitely to the theory of Wunderer (1910) that *S. maculosa* and *S. atra* in spite of these similar modifications are not closely related, it may be advisable to run ahead of our systematic

treatment at this point and make some comparison between the vasculated surfaces produced in other Amphibia for supplying oxygen to their young. In *S. maculosa* the larvæ usually remain enclosed within the egg-capsules. Respiration is carried on through these egg-capsules and four sets of greatly attenuated cells: namely, those of the parental capillary wall, the epithelium of the oviduct, the epithelium of the gills and the gill capillaries. There is no direct evidence that larvæ of *S. maculosa* receive nutriment from their parent's body. We shall see further along that in the marsupial frog, *Gastrotheca*, the tadpoles also remain within their egg-capsules and here, too, there is no evidence of the transference of nutriment from parent to young. The histological structure of the full pouch of *Gastrotheca* is very similar to that of the oviduct of the gravid *S. maculosa*. In the little frog, *Rhinoderma*, it is the vocal pouch of the male which becomes greatly attenuated and vasculated to form a respiratory surface. Burger (1905) concludes that nutriment passes from the capillaries of the pouch to those of the general integument of the tadpole's body. This may be true, but Burger's data is not conclusive. I have examined sections of the mature larvæ of *Rhinoderma* and find much yolk and no fecal matter in the digestive tract. It is apparent, however, that in many different groups of Amphibia large-yolked eggs may come in contact with various surfaces of their parent's body and these approximated regions become highly vasculated. If, as a further specialization, the yolk becomes reduced, the larvæ must either rapidly assume a larval habitus and emerge into the world or they may in one case apparently, (*S. atra*), make use of these respiratory surfaces for securing nutriment from the parent.

How may we be sure that in *S. atra* this loss of yolk is a further specialization? Why are not small-yolked eggs primitive? Various students have concluded on morphological grounds that *S. atra* is merely the high mountain form of *S. maculosa*. We shall see below that the small-yolked species of *Gastrotheca* are in all probability not primitive but have been derived from large-yolked types. In other words, forms with small-yolked eggs may have been derived from others with large-yolked eggs, or again, the reverse may obtain. Egg-size is usually not a criterion of relationship.

AMPHIUMIDÆ

This family, including only a single genus, *Amphiuma*, shows closer affinities to the Salamandridæ than to any other family, but it is certainly not directly derived from any recent genus. Also, its life history is not similar to that of any salamandrid but approaches that of some of

the plethodontids, which have been likewise derived from the salamandrids. The eggs of *Amphiuma* are laid on land; the capsules differ from those of any salamandrid or plethodontid. The larvæ hatch in a much more immature stage than they do in any terrestrial plethodontid; the external gills do not agree in detail with those of the plethodontids. The larvæ never throw off their larval habitus. *Amphiuma* is a "permanent larva" derived from some unknown genus. It is important to note that the eggs and larvæ of *Amphiuma* do not agree in detail with those of any other urodele. It may be stated that its life history approaches nearer to that of the plethodontids than to the cryptobranchids and sirenids with which it is frequently compared. *Amphiuma* possesses lungs and hence could not have been derived from any plethodontid. The similarity of life history between *Desmognathus fuscus* and *Amphiuma* is due to parallelism in divergent stocks having a common ancestry.

PLETHODONTIDÆ

The *Plethodontidæ*, the dominant family of American urodeles, embrace the most specialized of all salamanders. As Wilder and Dunn (1920) have emphasized, the family very probably arose in a mountain-brook habitat. The most primitive members of the group are found today in this habitat, although they occasionally live in springs in cold lakes or wherever the essential temperature and humidity factors of a mountain-stream bed occur. The *Plethodontidæ* have arisen from mountain-brook salamandrids, although apparently not from any modern genus. The eggs of the most primitive species agree closely with those of the mountain-brook salamandrids, notwithstanding the fact that they are sometimes deposited in springs instead of in swift streams. The eggs of *Gyrinophilus porphyriticus* have been described by Green (1925), those of *G. danielsi*, by Bishop (1924), and those of *Pseudotriton ruber*, also by Bishop (1925). They are laid on the under side of stones in flowing springs or slow-moving streams. Each egg is comparatively large, unpigmented, and attached separately by a gelatinous stalk. It is well known that *Eurycea*, which has been directly derived from *Gyrinophilus* or *Pseudotriton*, lays its eggs in a similar manner, but usually in a swifter current. *Pseudotriton montanus*, according to Brimley (1923, p. 82), deposits its eggs in small bunches attached to dead leaves in the outlet of springs. *Manculus*, which is a dwarf form directly derived from a southern race of *Eurycea bislineata*, attaches its eggs singly by short stalks to leaves in flowing spring water. The eggs may be grouped in small bunches on a few leaves or widely scattered among several leaves. Sometimes, as

I have noticed in animals breeding in the laboratory, the eggs break loose from their attachments and remain free among the leaves. As in the related forms, the eggs are comparatively large (2 mm.) and unpigmented. The primitive plethodontids, *Gyrinophilus* and *Pseudotriton*, as well as the genera immediately derived from this stock, *Eurycea* and *Manculus*, have apparently inherited the mode of egg-laying characteristic of the mountain-stream salamandrids. Is this evidence of genetic relationship or merely a case of parallel evolution in similar environments? In the case of *Dicamptodon* and *Rhyacotriton*, the only mountain-brook ambystomids, an anatomical analysis shows these genera to be related. Similarly, *Gyrinophilus*, *Pseudotriton*, *Eurycea* and *Manculus* are related and have similar habits. Apparently, therefore, the mode of egg-laying may remain constant while the adult structure is undergoing various modifications. This is exactly what is found to be the case in various other urodeles. Habits may be more constant in these instances than adult structures.

The mode of egg-laying is not entirely uniform throughout these plethodontids. Both *Manculus* and *Pseudotriton montanus* seem to move during the egg-laying process. Nevertheless, the form of the egg-capsule is the same in *Manculus*, at least, as in *Eurycea*, although the stalks are shorter. Two egg-capsules are present in *Manculus* in addition to the vitelline membrane. The larvæ of all the primitive plethodontids agree with the mountain-brook larvæ of other families as regards the adaptive characters discussed above.

The common dusky salamanders, *Desmognathus*, seem to have evolved directly from *Eurycea*, or, at least, they agree most closely with this genus osteologically. The large *D. quadra-maculatus* is the most primitive form of the group, as evinced by the fact that its skull structure is the least specialized. As shown by Pope (1924), it lays its eggs in the manner of *Eurycea*, although these may be in or out of water. *Leurognathus marmorata*, which has been directly evolved from *D. quadra-maculatus*, was found by Pope to have identical breeding habits. *D. phoca*, which is more terrestrial than *D. quadra-maculatus*, lays its eggs in the manner of the latter but, so far as known, always out of water. The eggs of *D. fusca* differ from those of *D. phoca* in that they are laid in the form of a rosary and are not attached singly. In this series of species, *D. quadra-maculatus*, *D. phoca* and *D. fusca*, a gradual change occurs from a condition in which the eggs are laid singly on the under side of stones in the water, as in *Eurycea bislineata*, to a condition in which the eggs are laid in a single string (or stringy cluster) at a short distance from the water.

In this evolution of the mode of egg-laying exhibited by the dusky salamanders, the most primitive method is evidenced by the least specialized species, and a progressive change accompanies the evolution of the adults. In another paper (Noble, 1927), it has been shown that this same series shows a progressive accentuation of certain secondary sexual characters. Is it mere coincidence that the one series should exhibit a progressive change towards terrestriality and dwarfism in the adult, and towards pronounced sexual dimorphism? A more terrestrial adult might be expected to lay its eggs in a drier situation than would an aquatic one, although this does not hold true for our other urodeles. Terrestrial eggs, however, necessitate an early larval life radically different from that found in aquatic ones. The detailed morphological and

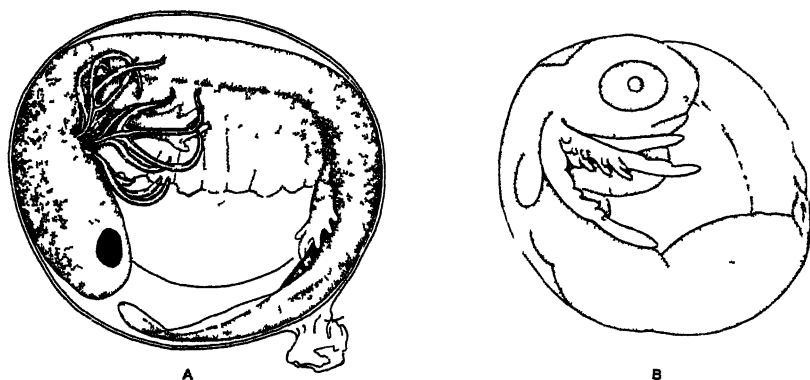


FIG. 4—Plethodontid larvæ: (A) *Desmognathus quadra maculatus*, mature larva a few days before hatching; (B) *Hemidactylum scutatum*, same stage, showing difference in yolk volume, gill form and limb development.

physiological changes have not been described for this series. The eggs of these species I have found were difficult to raise in the laboratory.

The larvæ of the more terrestrial species, such as *D. fuscus*, after a short life on land (Wilder, 1913) make their way to the streams, where they soon take on the larval habitus of their more aquatic relatives. The later larvæ of *D. quadra-maculatus*, *D. phoca*, *D. fuscus carolinensis* and *Leurognathus* are nearly identical as to general form and proportions and the character of the gills. Only slight specific differences separate the larvæ. The larvæ, while within the egg-capsules, have the long thread-like gills shown in Fig. 4 A. When the larvæ escape into the water, these gills become shorter and form a small bunch on each side of the neck. There is never a central ramus with a fringe of filaments as in the more primitive plethodontids. The shortness of these gills is

probably correlated with the swiftness of the current, which does not mold the gills but merely places a limit on their extent in length. Thus even the most primitive species of the genus, which lay their eggs in the manner of *Eurycea*, differ from that genus in the form of their larval gills. Certain larval features are, therefore, present in *Desmognathus* and *Leurognathus* that stamp the species as a natural group distinct from the ancestral stock occupying the same habitat.

A second change has occurred in the evolution of aquatic plethodontids which seems at first glance highly adapted to the needs of the terrestrial embryo. The aquatic eggs of most urodeles, such as *Ambystoma*, are surrounded by two coats of jelly, which evidently serve to protect the growing embryo. It is apparent from a study of the female urinogenital organs that the inner capsule is secreted by the oviducal glands, the outer by the cloacal glands. These two sets of glands are carried over to the aquatic plethodontids, as shown by Kingsbury (1895). I have found them present in *Munculus* and have readily differentiated two capsules surrounding the egg even though both are comparatively thin. The larvæ of all forms laying their eggs on land are provided with large external gills. In *D. fuscus* only one egg-capsule is present (in addition to the vitelline membrane). This would seem to be an adaptation to aerial respiration. But *D. quadra-maculatus*, I find on sectioning, lacks both female cloacal glands and the outer egg-capsule. Thus, the external form of an egg is not controlled by the number of capsules, for their eggs are like those of *Eurycea* and other primitive plethodontids which have the double capsules.

Naturalists in describing the eggs of Amphibia usually report the number of egg-capsules present. This is a very difficult and, in some cases, a useless task. The fresh eggs of *D. quadra-maculatus* seemed to have two capsules but, when these were sectioned, only a single thick one with a lightly differentiated inner surface was found.

The terrestrial *Batrachoseps attenuatus* has been described by Snyder (1923) as having three capsules in addition to the vitelline membrane. My sections of the cloaca of this form show that no glands are present. Thus, it is probable that in *Batrachoseps*, as in various terrestrial Salientia, the egg-capsule may be peeled off as a number of complete parts but these can hardly be called capsules. It may, at least, be concluded that all terrestrial plethodontids lack the female cloacal glands (a rudiment occurs in *Hemidactylium*, Dieckmann, 1927). In the genus *Desmognathus* these glands are lost, while the egg-laying is still primarily aquatic. In this character of the adult the primitive species of *Desmog-*

nathus would seem to be preparing for the future terrestrial mode of egg-laying.

The most primitive of the completely terrestrial plethodontids is the familiar American genus *Plethodon*. The latter differs from *Desmognathus* in its less ossified vertebræ, more complete and less specialized skull. It was, therefore, not directly evolved from *Desmognathus*, but it is more closely allied to this genus than to any other aquatic plethodontid. The eggs and young of certain species of *Plethodon* are well known. Those of *P. cinereus* have been described by Piersol (1910, 1915), Cochran (1911), etc.; those of *P. vandykei*, by Putman (Noble, 1925). The eggs of the known species of *Plethodon* are purely terrestrial, being laid under or in logs away from the water. I have found the eggs of *P. cinereus* under the boards of a plank road. The egg-capsules, the method of attachment, and the form of the embryo appear identical in all species of the genus. The young undergo a direct development within the egg-capsules and hatch fully formed. They respire within the egg-capsule by three gills fused at their base into a single trunk. The gills branch in the manner shown for *P. vandykei* (Fig. 2 C). The immediate ancestor of *Plethodon* may be lost, but it is instructive to compare its life history with that of *Desmognathus*. It would not require very much modification of the encapsuled larva of *Desmognathus* to produce an embryo such as that of *Plethodon*. A thickening of the gills and a speeding up of development would be the chief requirements.

Whatever may have been the immediate ancestry of the terrestrial *Plethodon*, we may feel certain that it has been the stock from which a number of other plethodontid genera were immediately derived. Fortunately, the life histories of most of these derived stocks are known. In the eastern United States *Hemidactylium* was evolved from *Plethodon* merely by the loss of a fifth toe. In *Manculus* among the plethodontids, in *Salamandrina* among the salamandrids, and in several hynobiids, this loss of the toe is not accompanied by any great modification of adult structure or of life history. In the West, *Batrachoseps* was derived from *Plethodon* by a similar loss but, in addition, the skull was somewhat modified and the body elongated. And in the West, *Ensatina* and *Aneides* were evolved but in other directions. The first is practically identical with *Plethodon* except for its constricted tail. The skull of the second is greatly modified by a fusion of the premaxillaries, the elongation of the maxillary teeth, and is molded by the powerful temporal muscles which give *Aneides* a peculiar appearance. These four genera are all terrestrial; they lay their eggs on land. The egg-capsules of *Ensatina*,

it is said, lack peduncles while those of *Aneides* are long and twisted. The eggs do not develop in exactly the same way in all the genera. *Aneides* and *Batrachoseps* possess leaf-like or "stag-horn" external gills which in general pattern are similar to those of *Plethodon* (Fig. 2 C), but which differ in form due to an increase or diminution of gill tissue. In *Aneides* the horns are very broad, giving a leaf-like form. In *Batrachoseps* the horns are reduced to three branchless spikes, united at the base as in *Plethodon* and, therefore, differing from the gills of the more primitive plethodontids. How may we account for this difference in gill form between the close relatives *Aneides*, *Plethodon* and *Batrachoseps*? Emmel, V. E. (1924, p. 372) has shown that this apparent reduction of the respiratory surfaces in *Batrachoseps* is compensated by . . . "an increased surface exposure of hemaglobin for gaseous exchange, through the substitution of flattened nonnucleated cytoplasmic discs for typical nucleated amphibian red blood corpuscles."

Aneides and *Batrachoseps* hatch fully-formed from the egg-capsule. The egg-capsules have been described as single in *Ensatina* (Storer, 1925) and triple in *Batrachoseps* but, as stated above, this difference may be a matter of interpretation. Except for the variation in gill form there is no essential difference in egg, embryo or life history between these genera on the one hand and that of *Plethodon*, the stock from which they were derived, on the other.

Hemidactylium differs structurally slightly from *Plethodon*, much less than do *Aneides* or *Batrachoseps*. Further, it is apparently a derived not an ancestral genus, for it may be shown that most urodeles which possess only four toes have arisen from and not given rise to five-toed forms. Again, we should naturally assume that all ancestral stocks would have a more complete set of toes, skull elements or other morphological parts than would genera derived from them. The life history of *Hemidactylium* has recently been made known through the researches of Bishop (1919) and Blanchard (1923). Both of these authors carefully avoid a discussion of the "taxonomic isolation" (Blanchard) of *Hemidactylium*. The life history of this genus seems at first sight quite different from that of *Plethodon*. Although the eggs are laid on land, they are deposited very near the water, and the larvæ hatch out in a very immature condition. Bishop (1919, p. 266) concludes:

The large number of eggs deposited, their intimate relation to sources of moisture and early absorption of the yolk, indicate recent adaptation to terrestrial life.

Such a conclusion would not agree with the anatomical data, for *Hemidactylium* is immediately derived from the terrestrial *Plethodon*. Two explanations have been offered for this peculiar state of affairs. Dunn (1926 b) inclines to the belief that the *Plethodon* was originally aquatic or, at least, laid eggs in the manner of *Eurycea*, and that the life history mode of *Hemidactylium* is a retention of this primitive condition. On the other hand, it has been shown (Noble, 1925) that reduction of the yolk which has obviously occurred in certain frogs, such as some marsupial frogs (*Gastrotheca*), went hand in hand with an increase in the number of eggs and the early reappearance of the typical polliwog characters. In short, the peculiar life cycle of *Hemidactylium* was forced upon it by a reduction of the yolk content of the eggs. An apparent objection to the second point of view is that the egg size of *Hemidactylium* is not greatly reduced. How much this is due to the absorption of water it is impossible to say. The early larva of *Hemidactylium* while within the egg-capsule has a far smaller supply of yolk than has *Plethodon* (Fig. 4b). Thus, the second theory receives some support from conditions found in the tree frogs, while the first is without this advantage.

The larva of *Hemidactylium* is unique among the Plethodontidæ in possessing a dorsal body fin. But as this is the only plethodontid larva which inhabits ponds or large bodies of still water, the reappearance of these *Ambystoma*-like structures might be expected. *Hemidactylium* does not, however, redevelop a balancer or the disharmonic digits of *Ambystoma*. So far as is known, only this one of the "pond-type characters" appear. When all facts are considered, it seems most likely that the dorsal fin is a new, not an atavistic or a retained character in *Hemidactylium*.

There remain three genera of terrestrial plethodontids to discuss. These—*Hydromantes*, *Oedipus* and *Oedipina* are apparently closely related, although the first genus is widely separated geographically from the latter. *Oedipina* is an elongate *Oedipus*, just as *Batrachoseps* is an elongate *Plethodon*. In this *Oedipus-Hydromantes* group, as elsewhere in the salamanders, we find a remarkable agreement of structure and life history. *Hydromantes*, *Oedipus* and possibly *Oedipina* (to judge from the thick oviducts) give birth to their young alive. They are the only ovoviparous plethodontids.

How did ovoviviparity arise in the Plethodontidæ? In the Proteidæ we found that it was merely a matter of the response on the part of the maternal parent to an adverse environment. Similarly, in the Sala-

mandridæ. the mountain life may have had some effect in producing ovoviviparity in *S. maculosa* and *S. atra*. We use the word "produce" advisedly since in *Salamandra* the length of larval life within the parent is correlated with external factors. *Hydromantes*, *Oedipus* and *Oedipina* show close affinity to *Plethodon*. The two latter genera have their center of dispersal in Central America. Given a *Plethodon* stock residing in the mountains of Central America and subjected to adverse conditions, ovoviviparity may have arisen, just as it did in more primitive groups under similar environmental conditions. This does not necessarily imply an adaptive effort on the part of the salamander. It is conceivable that natural selection alone could produce these results. It would be interesting to know how closely the intrauterine larvæ of *Oedipus*, *Oedipina* and *Hydromantes* agree with the terrestrial, encapsuled larvæ of *Plethodon*.

In an earlier paper (1921) I have expressed the view that *Oedipus* was closely related not to *Plethodon*, but to *Eurycea*. The free tongue of *Oedipus* is found in the latter but not in the former genus. Further, as *Desmognathus* nearly bridges the gap between aquatic and terrestrial species, why could the immediate ancestors of the terrestrial *Oedipus* and *Hydromantes* not be semi-aquatic forms such as *Eurycea*? This possibility should not be overlooked, but aside from the character of the tongue and the identical secondary sexual characters, *Plethodon* has nearly as much in common with *Oedipus* as *Eurycea* has. Further, the attached tongue seems to be a larval character retained in many genera such as *Desmognathus*, *Stereochilus*, etc., which have undoubtedly arisen from free-tongued forms. The matter cannot be decided at this moment. A detailed knowledge of the development of *Oedipus*, *Oedipina* or *Hydromantes* might throw considerable light on the subject.

In conclusion, we may glance back over the life histories reviewed and draw certain generalizations. Related groups of urodeles usually exhibit a similar mode of life history. Pond, mountain-stream and terrestrial larvæ represent three distinct adaptive types. Urodeles have not often changed from pond to land-breeders or back to mountain-stream forms. The evolution of the mode of life history has been very slow and usually the adult has changed its organization—that is, one genus has changed into another before any change of life history has taken place.

GYMNOPHIONA

GENERAL DISCUSSION

Unfortunately, the caecilians cannot be discussed in detail for the interrelationships of the genera have been determined in only a very few cases. Those who are most familiar with the group admit the inadequacy of the existing classification, based largely on superficial characters. Peter (1908) deplored this state of affairs. His suggestions as to the probable fundamental characters are most valuable and should be investigated throughout a large series of genera. In the present connection we may discuss these genera only in the broadest terms.

The most primitive genera are those that possess scales, that exhibit the fewest fusions of skull elements and are the least modified for burrowing. *Ichthyophis* in the East Indies, and *Rhinatrema* in South

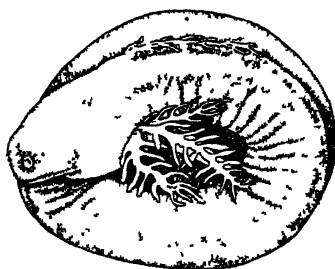


FIG. 5.—Encapsuled larva of *Rhinatrema peruvianum*.

America, possess these characteristics. The life history of *Ichthyophis*, thanks to the researches of the Sarasins, is well known. The female lays her eggs on land in a burrow. The encapsuled larvæ have three pairs of feather-like gills, which are lost when they leave the capsules to take up a larval life in the water. This life history has been compared many times with that of *Amphiuma*, *Desmognathus* and other urodeles that lay their eggs on land. The details, however, differ. The caecilians are an ancient and in many ways degenerate group. It is probable that they have come by this terrestrial habit through steps as gradual even if these be not similar to those of the plethodontids. It should be noted that no caecilian has a less specialized life history than that of the most primitive genera.

The life history of *Rhinatrema* is unknown. In the American Museum of Natural History there is a single female specimen of *Rhinatrema peruvianum* sent from Juliaca, Peru, by Mr. H. H. Keays, and this speci-

men is accompanied by a string of eggs containing embryos very well formed. It will be noted from the figure (Fig. 5) that these encapsuled larvæ are very similar to those of *Ichthyophis*. It is probable that the life histories of the two genera are similar.

A genus more closely allied to *Ichthyophis* than *Rhinatrema* is *Hypogeophis*. Its life history is very similar to that of the former except that the aquatic larval stage is eliminated. There is no way of determining whether *Rhinatrema*, too, avoids the aquatic stage.

The derived genera of caecilians are those that lack scales. The aquatic *Typhlonectes* belongs in this category. *Typhlonectes* has gone one step beyond *Rhinatrema* in the same way that *Oedipus* has advanced over *Plethorlon*: it retains the egg within its oviducts and gives birth to living young. The larval gills of *Typhlonectes* have fused into a plate on each side in order better to supply the embryo's needs.

The life histories of *Ichthyophis*, *Hypogeophis* and *Typhlonectes* agree fully with the hypothesis advocated above—namely, the gradual change in life history accompanying adult specialization. However, some difficulties arise when we examine the other genera. *Dermophis* is primitive and yet ovoviviparous. *Siphonops* is both ovoviviparous and oviparous. The embryo of the ovoviviparous species possesses gills similar to those of *Typhlonectes*. The case of *Siphonops* may possibly be explained when the adult structure of *Siphonops annulatus* and of *S. brasiliensis* is better known. The limits of the genus *Siphonops* are not well established.

SALIENTIA

The frogs and toads exhibit the most "unusual" modes of life history. They possess many specializations of ontogeny which have been discussed many times. Unfortunately, for a clearer understanding of the evolution of the various groups these peculiar habits and modifications have been looked upon usually as mere oddities of nature and even specialists have recently declared that they have no bearing on a natural grouping of the various genera.

When I was recently revising the classification of the frogs and toads (Noble, 1922, 1925), it came forcefully to my attention that specializations of life history, just as specializations of adult structure, were often of value as indicators of relationship. *Protopipa* and *Pipa* are the only frogs which carry their eggs in individual dermal chambers on the back; *Phyllobates* and *Dendrobates*, the only genera which transport their unspecialized tadpoles to the stream; *Cryptobatrachus*, *Cerathyla*, *Gas-*

trotheca and *Amphignathodon*, the only ones which carry their eggs in a single mass on their backs (either exposed or enclosed in a dermal fold). Further, the last group of genera have larvæ characterized by distinctive bell-shaped gills. The relationships of the above genera had been for some time open to dispute, for the members of each group differed the one from the others in matters of dentition, and teeth characters were previously considered of primary importance in the classification of the order. But in these cases and in many others (Noble, 1925) it seemed that life history gave the additional evidence needed to confirm

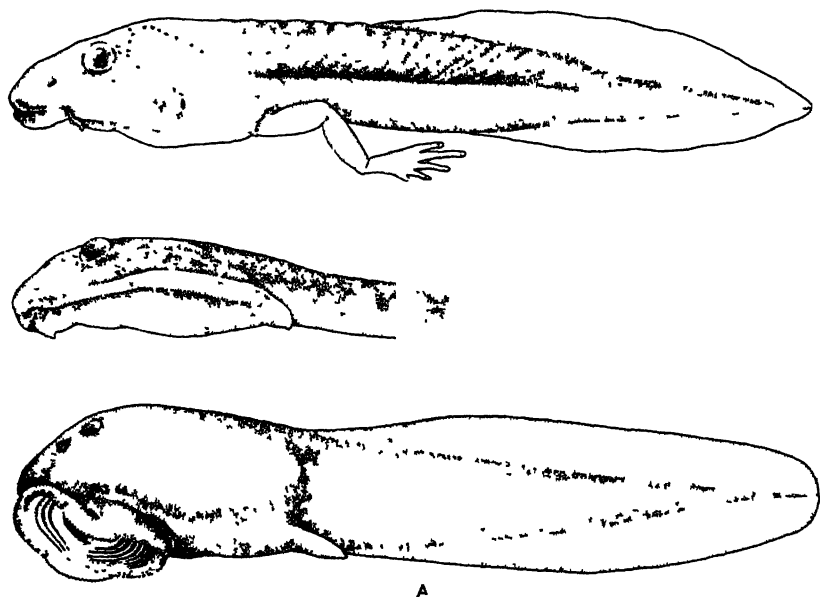


FIG. 6—Mountain-brook tadpoles: (A) *Ascaphus truei*; (B) *Borohucetes petiopolitanus*; (C) *Astylosternus robustus*.

the conclusions based on all the available anatomical data that each of the above groups was actually a natural one.

The mode of life history does not always give proof as to the relationships of a group. Frequently, as in the case of our common *Rana*, this is unspecialized and, while certain details of the breeding habits or development may afford data as to the mutual relationships of the various species, it is difficult to find features sufficiently distinctive to be used in showing the relationship of *Rana* to other genera. Further, very little is known about the life history of most Salientia. It would perhaps be of value for future work to include in the following discussion

all the known details of life history which have been described. This would, however, obscure the fact that some of these features are of value in phylogenetic studies at the present time while others may become so only when further details are forthcoming. In the following account emphasis has been laid, therefore, on only a few characters, and no attempt is made to give a complete picture of the life history of any one form.

LIOPELMIDÆ

The life histories of *Liopelma* and *Ascaphus*, the only two genera in the most primitive family of frogs, do not agree with that of the Discoglossidæ nor with each other. The latter state of affairs would seem at first glance disastrous to the theses expressed above. *Ascaphus* lays its eggs in the water of cold mountain torrents, *Liopelma*—on land. The eggs of the first develop into tadpoles extraordinarily modified to life in the torrents, while those of the latter develop directly into frogs. If we look back over the urodeles, this seems an enormous difference, but if we glance forward over the Salientia, we shall see how readily tadpoles have assumed a mountain-brook habitus (see Fig. 6. and especially Plate IX). *Liopelma* and *Ascaphus* are separated geographically by an enormous distance. They represent the relics of a former wide-ranging stock. Their geographic isolation and their undoubted antiquity would foster the genesis of special modes of development. When we have examined other groups of frogs, it will be apparent that the differences which separate *Liopelma* and *Ascaphus* are not so fundamental as they seem; similar differences appear among the genera of other families.

On the other hand, both *Liopelma* and *Ascaphus* show in their eggs and larvæ certain characters which are indicative of their relationship. The eggs of both genera are proportionately very large. The ovum measures 4.5 mm. in *Ascaphus* and 5 mm. in *Liopelma*. They are both unpigmented, and exhibit during the late gastrula stages great similarity. Thanks to the kindness of Mr. Archey, I have examined some of his original material of *Liopelma* and am able to add some details to his description. The developing embryo of *Liopelma* is well raised from the yolk in very much the same way as in *Ascaphus*. According to Archey's description, *Liopelma* never develops gills. There is, however, a distinct suggestion of the three branchial arches not shown in Archey's Fig. 1. At this stage it is too early to expect diagnostic characters. It may be noted, however, that there is a much closer resemblance between the early embryos of *Ascaphus* and *Liopelma* than exists between either of these and some of the higher types (Fig. 7).

Archey (1922) has compared his hatching *Liopelma* with the corresponding stage of *Eleutherodactylus martinicensis* and *Rana opisthodon*. The chief characters that Archey finds to distinguish them—namely, the external gills of the first and the respiratory folds of the second—have been incorrectly described and are not so different as Archey believes.

Liopelma differs, however, during its development from all higher types which have direct development by the following characters:—(1) the eggs are grouped in small clusters surrounded by a common capsule of soft jelly (apparently as in *Ambystoma*); (2) the front legs develop earlier than the rear pair; (3) the tail is more muscular and narrower than in *Eleutherodactylus*, etc.; (4) the egg-tooth is lacking (it is pos-

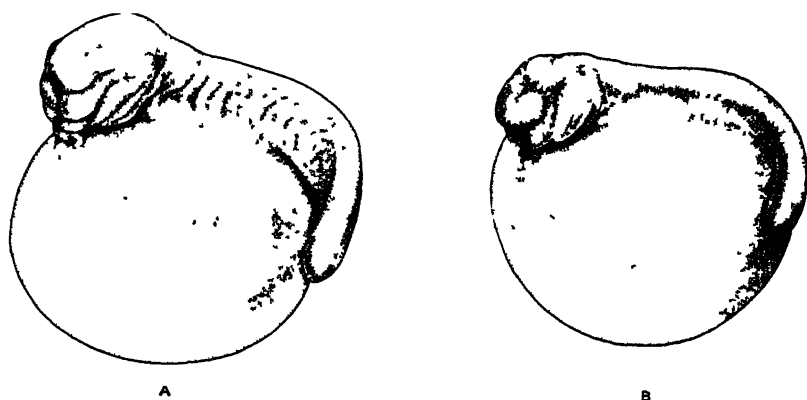


FIG. 7.—Early liopelmid embryos: (A) *Ascaphus truei*; (B) *Liopelma hochstetteri*.

sibly also lacking in certain East Indian Brevicipitids); (5) hatching is a slow process, correlated with the disintegration of the capsules; (6) the tail is absorbed slowly after hatching. These differences make it probable that the method of direct development in *Liopelma* has been acquired independently from that in the higher groups. This suggests that primitive Salientia had large eggs that went through a larval development in the water. In other words, *Ascaphus* probably represents a more primitive method of development than that of *Liopelma*.

The larval life of *Ascaphus* is, nevertheless, very specialized. The tadpole is, in fact, more thoroughly modified for life in a mountain torrent than are any of the "mountain-brook tadpoles" of the higher genera.

The life history of *Ascaphus* has been studied by Gaige (1920). I have been so fortunate as to secure the services of Mrs. Gaige's guide

and field assistant, Mr. Phillips Putnam, to continue the work. Putnam has sent me living specimens of both adults and larvæ across the continent packed in boxes of dripping ice water. In this way I have been able to supplement the field observations of Gaige and Putnam.

The general habits of the adult and larval *Ascaphus* may be briefly outlined. I quote from the field notes of Mr. Putnam:—

Ascaphus may be found in any of the small, snow and spring-fed streams of the Olympic Mountains. They are very partial to swift, cold water. The first *Ascaphus* that I found were hiding under submerged stones in these little creeks. When the stones were raised, the *Ascaphus* would frequently remain motionless and were exceedingly hard to see because of the swiftness of the water. In many instances I found it necessary to resort to feeling for them. Their color, which varies from light grey to brown or coppery red, blends almost perfectly with the stones and sticks which cover the bottom of these creeks. Frequently, the swift water would dislodge them and wash them downstream when I was not quick enough to seize them. Occasionally they are to be found swimming leisurely in the pools or crawling on the banks.

Last summer, when collecting near Elk Creek, a fairly large and turbulent creek about five feet in width, I came to a bluff or mossy rock near the creek. Over it a few trickles of water flowed. I climbed it and secured eight or ten *Ascaphus*. They were resting on the damp moss. When they saw me, they attempted to dart away by leaping.

During rainy weather, I have found it hard to secure them in the creeks. At such times they are most commonly away from the water. Until last fall, I had always thought that *Ascaphus* never left the forests during warm weather, as with very few exceptions I had always noted them in shaded streams or, when away from the water, in the cool shade of dense coniferous forests. On September 10, 1923, I was collecting at the Black and White Camp at an elevation of 4500 feet. At noon I returned to camp and sat down in a patch of blueberries to eat my lunch. The blueberries were the small mountain kind that never grow more than a foot high at most. I heard a slight rustling some fifteen feet away. On looking in the direction of the sound, I saw a frog crawl leisurely through the grass and blueberries. I watched it for some time and then went over and picked it up. To my surprise I found it to be a fat, well-fed *Ascaphus* that had apparently come out into the meadow to feed on the abundant insects. This is the first record, so far as I know, of an *Ascaphus* being found in an open meadow in broad daylight, apparently feeding. The surrounding country was timbered, but a few hundred feet above my camp the timber line was apparent. Near my camp were a number of small streams frequented by *Ascaphus*.

Ascaphus appears to be neither strictly diurnal nor nocturnal. When collecting at night with an acetylene lamp, I have found the frogs under practically the same conditions under which I have observed them during the day. They were hiding under the stones and some were hopping about the creeks.

In these creeks their unmistakable tadpoles may usually be found. The largest of them are about one and a half inches long. They may commonly be

seen clinging to the stones in both the turbulent and still section of the creek. They will fasten themselves so securely to the stones with their large suckers that it is hard to remove them without inflicting injury. The tadpoles which I secured in June were fairly large, the largest being about one and three-eighths of an inch in length. By August 18, these tadpoles had practically transformed into perfect little frogs about half an inch in length. During August and September I came upon the smallest tadpoles of any that I noted last summer. It seems likely that the *Ascaphus* eggs are hatched during August and that the tadpoles winter over to transform into minute frogs during the latter part of August and the early part of September of the following year.

The tadpoles which Mr. Putnam sent me I have kept alive for weeks in glass vessels over which ice water dripped. When the vessels were disturbed, the tadpoles frequently pushed their heads out of the water and attached their suckers to the sides of the vessel. I thought at first that this might assist them in their respiration, but injected specimens show that this anterior part of the head and sucker are not so vasculated as the middle or posterior sections of the sucker, nor nearly so vascular as is the tail.

The tadpoles have a simple but efficient mechanical device for controlling the flow of water into the buccal cavity. The nostrils are produced into irregular funnels (Fig. 8). When a strong current is forced with a pipette against these funnels, they bend down and close (Fig. 8 B). When the tadpole thrusts its head out of water, they close by their own weight. I know of no other tadpole equipped with such structures.

No water passes into the buccal cavity through the mouth of the tadpole of *Ascaphus*. At least, numerous efforts to demonstrate currents with carmine fail to show any such currents. The tadpole moves usually by opening its mouth and bringing its lower jaw up to its upper. When the tadpole is moving normally, it hitches forward at about one movement every one to one and one-half seconds. The opening of the mouth is not synchronous with the heart beat, which proceeds more quickly. When disturbed, the tadpole releases its hold and swims rapidly across the vessel to take up a new hold and hitch forward again as before. Sometimes it will hitch forward until out of water but usually it follows the sides of the vessel.

The tadpole of *Ascaphus* apparently takes in most of its food through its external nares. Strong water currents pass in through the funnel nostrils and out through the median spiracle. Comparatively large particles—as large as the majority in the tadpole's stomach—are carried in this way. The largest I saw carried down the funnels measured 1 mm.

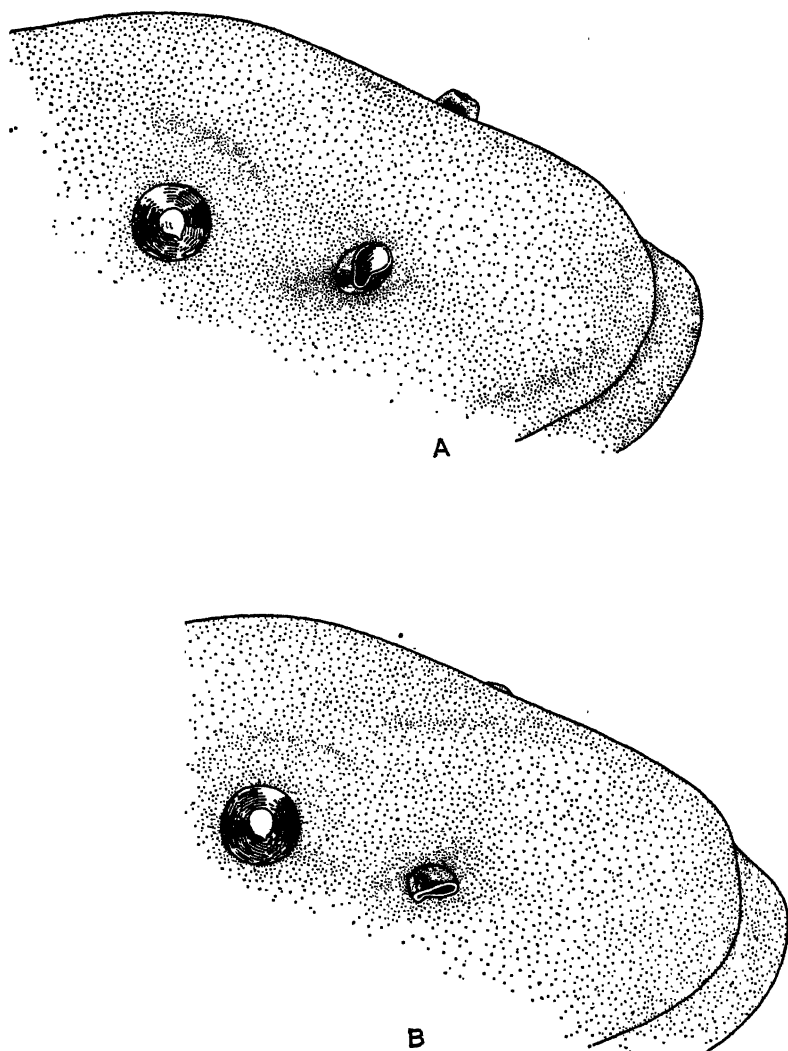


FIG. 8.—Nasal valve of the larva of *Ascaphus truei*: (A) in quiet water; (B) in swift water.

x .25 mm. Undoubtedly, some particles are scraped off the vegetation on the rocks as the tadpole moves along. But only the lower mandible would function in this process and this structure is exceedingly small (Fig. 9).

All tadpoles taken in the field exhibit a broad white margin to the upper mandible. This upper mandible, unlike that found in any other

species, is merely a flat horny plate. Sections reveal, however, that the fundamental characteristics of a tadpole's mandible are not lost in *Ascaphus*: in other words, the upper mandible is not a sheath of cornified epidermis, but is formed of a series of cones exactly as the beak of our common tadpoles (Fig. 9 B). The white margin is not the true edge of the mandible but is formed by adjacent non-cornified epidermal cells lying caudad to the mandible. These relations are shown in the figure.

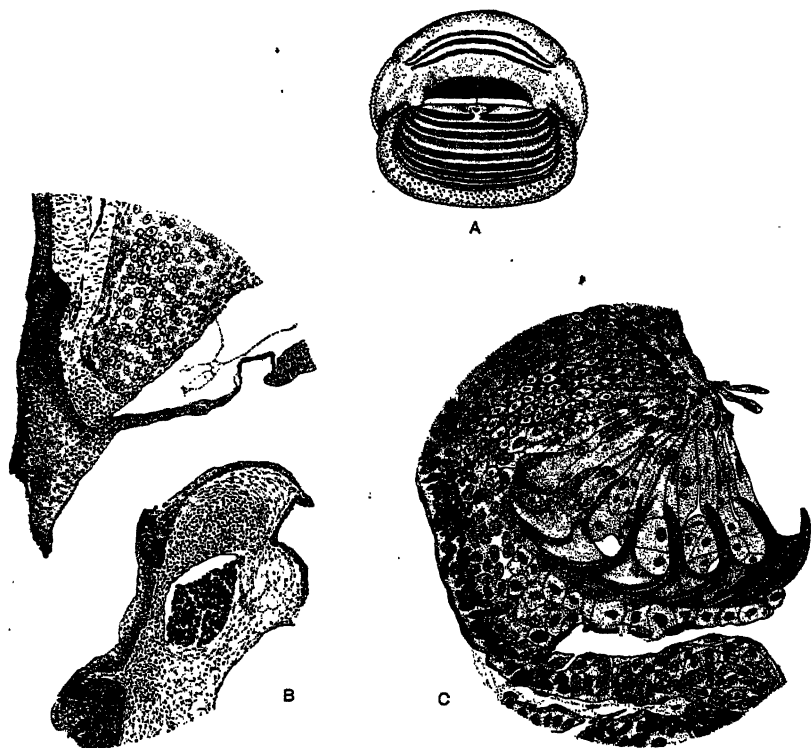


FIG. 9.—Buccal apparatus of *Ascaphus truei*: (A) mouth of larva, ventral aspect; (B) sagittal section of mandibles, $\times 50$; (C) a sheath of larval teeth, sagittal section, $\times 240$.

Tadpoles which were kept in glass aquaria for more than a week lost the white margin to the upper mandible. This was caused by the fact that the beak of horny cells grew down over the non-cornified epithelium. In nature this horny edge is kept worn down so that the upper mandible is far forward of the mouth. These relations, so different from those in any other tadpole, are represented in Fig. 9.

Gaige (1920) described the chief peculiarities of the tadpole of

Ascaphus. They may be further seen in Figs. 6 and 9. The crypts which Gaige mentions are caused, I find, by the ducts of poison glands. These glands, of the ordinary granular type, are scattered irregularly over the body. My sections show that there are no multicellular mucus glands. Such conditions have considerable theoretical importance. As all the integumental glands, even the smallest, are of the typical granular type, they could not have arisen from mucus glands. Various attempts have been made to demonstrate that all integumental glands arise from mucus glands. The conditions in *Ascaphus* would support the view that mucus and poison glands are of two fundamentally different types. Poison glands have been demonstrated in the integument of other tadpoles (see the summary by Phisalix, 1922, p. 22). Those of *Ascaphus* differ from the glands of these other tadpoles (species of *Rana*) in being more diffuse, less concentrated into groups.



FIG. 10.—Mouth of the larva of *Rana rugulosa* dissected free and showing both jaws in the same plane. The lower jaw is on the right.

Most of the peculiarities of the *Ascaphus* tadpole adapt it directly to its life in the mountain torrent. It may be interesting to summarize these adaptive features: (1) body flattened, tapering, the abdomen provided with a posteriorly projecting flap (compare with *Borborocoetes petropolitanus* (Fig. 6 B), (2) no body fin, that on tail narrow, (3) mouth modified into an enormous sucker (Fig. 6 A) provided with numerous glandular warts and rows of teeth, (4) upper mandible a flat plate, lower vestigial (Fig. 9 A), (5) folds in sucker arranged to permit opening of the mouth (for locomotion) without seriously detracting from the suctorial nature of the apparatus, (6) external nares produced into funnels which bend down in a swift current and prevent flooding of buccal cavity, (7) lateral line system and pineal eye spot not visible, (8) lungs absent during the greater part of larval life.

The tadpole of *Ascaphus*, although extraordinarily adapted for life in a torrent, still retains some external evidence of its relationship, not to *Liopelma*, for that genus skips over the aquatic stages, but to its next of kin,—the Discoglossidæ. The larval teeth are modified in order the better to grip the irregularities in the rocks to which the larva holds. They are arranged in part in double rows both anterior and posterior to the mouth. Such double rows of larval teeth are found elsewhere only among the Discoglossidæ, although one ranid, *Rana rugulosa*, has a double set of alternating teeth to each row (Fig. 10).

A second feature worthy of special note is that the teeth retain, in spite of their strong bracing and, hence, flaring of their bases, the simplicity of structure characteristic of discoglossids, pelobatids and a few bufonids, and ranids. The larval teeth of all discoglossids are entire, not denticulated as in *Rana* and most higher frogs.

Alytes exhibits an incipient denticulation, which is of a simpler type than that of higher forms. I have found entire teeth to be characteristic of all pelobatids that have larval teeth. The bufonids, *Pseudis paradora* and *Ceratophrys dorsata*, also have spike-like teeth. In the latter species the teeth are very strong, almost tusk-like and probably owe their form to a secondary modification. The vast majority of the bufonids and all hylids, ranids and brachycephalids which have been examined by me possess larval teeth of the denticulated type. Hence, the simple structure of the teeth of *Ascaphus*, if not diagnostic of discoglossid relations, is, at least, indicative of its lowly position among the Salientia.

DISCOGLOSSIDÆ

The bell toads, or Discoglossidæ, are typically aquatic species. Like most pond-breeding urodeles and Salientia, they have small-yolked eggs, and these undergo the usual polliwog development of *Rana*. Are these eggs primitive or are they secondarily deprived of their yolk? Judging from the conditions in *Ascaphus*, this would seem to be a secondary reduction. Further, there are several other cases in the Salientia where the yolk has been secondarily diminished. It is possibly because of this frequent fluctuation in yolk size that the mode of life history in the Salientia is so much more variable than in the Caudata. There are, however, certain features distinguishing the breeding habits and larvæ of the Discoglossidæ which are found elsewhere only in the Pelobatidæ or among scattered genera of higher families. These are the lumbar amplexus, the median spiracle and the larval tooth form. The life history of *Alytes* comes more into the scope of this discussion, as it is usually

considered very specialized. Only this genus will be mentioned, therefore, in further detail.

The large size of the eggs of *Alytes* may represent the retention of a liopelmid character. The exact relationships of *Alytes* to the other discoglossids is not known. The egg-capsules (exclusive of the vitelline membrane) of *Alytes* are two in number. The eggs are connected with each other by narrow threads of gelatinous material. Eggs of *Ascaphus* exhibit similar conditions, except that the connecting threads are thicker and shorter. It would be interesting to know more of the eggs of *Ascaphus* through field observation.

The encapsuled larva of *Alytes* differs in several particulars from similar larvæ of higher frogs. The single pair of external gills is not the result of fusion as in *Plethodon*. These gills arise from the most anterior pair of gill arches. They also exhibit a peculiar stag-horn form not found in air-breathing gills of other frogs. The tail of the encapsuled tadpole is not greatly expanded or thinned although the larva is devoid of external gills several days before hatching. The tail is more vasculated than in aquatic tadpoles, but it is not excessively flattened. It may be compared with the tail of the larval *Liopelma* and contrasted with the larval tails of certain terrestrial bufonids and brevicipitids.

Finally it may well be emphasized that the peculiar brooding habits of *Alytes* are not found in any other Salientia.

PIPIDÆ

The Pipidæ are found today only in Africa and South America, and the genera on the one continent form a group anatomically distinct from that on the other. It is perhaps not surprising after our examination of the Liopelmidæ to discover that the life histories of the African genera so far as known are very unlike those of the South American genera. *Xenopus*, the more primitive genus in Africa, lays its eggs in a manner not unlike *Bombina*. The Pipidæ have apparently arisen directly from aquatic discoglossids but not from any recent genus. The tadpole, so excellently described by Bles (1906) and Dreyer (1915) is unique among Salientia. Bles has tried to discern in the development of *Xenopus* certain urodele features. These features seem to me to be directly dependent on a diminished amount of yolk and a precocial development of the frontal or hatching gland.

One feature of the early larva of *Xenopus* deserves special mention. The adhesive organ of this genus is of a peculiar form, quite unlike that of any of the higher frogs but very similar to that of *Bombina*.

The form of the adhesive organ, although not always diagnostic of natural groups, is usually the same in related groups.

Pipa, the most primitive South American genus, has excited the wonder of observers of nature for nearly three hundred years. Its eggs are much larger than those of *Xenopus*. The details of development are known only in part, but these are sufficiently unlike those of higher egg-carrying frogs to prevent us from making any direct comparisons between them.

All frogs that carry their eggs on their back may be placed in one of two categories: (a) those that have their dorsal integument modified to aerate the eggs, and (b) those in which the integument remains unmodified. To the first group belong *Protopipa*, *Pipa* and *Gastrotheca*, to the second belong a number of genera which we shall discuss later on. *Protopipa* and *Pipa* have arisen from stocks totally different from those that gave rise to *Gastrotheca*, and the details of their larval and adult specializations are very different. They are not, however, as different as the published descriptions usually indicate. All frogs that carry their eggs surrounded by maternal (*Protopipa*, *Pipa*, *Gastrotheca*) or paternal tissue (*Rhinoderma*) exhibit only one peculiarity of the parental tissues. The epidermis or epithelium surrounding the eggs is much attenuated and vasculated.

The details of how the dorsal integument grows up to enclose the eggs of *Pipa* are unknown. Similarly, no one has observed how the eggs are placed in the dorsal pouch of *Gastrotheca*. Sections show that the egg pouches of *Pipa* and the full sack of *Gastrotheca* are very similar histologically. So far as can be determined by a histological examination, both integuments are modified only by a vascularity and thinning. I do not believe any mysterious mechanism is necessary to account for the different modification of the female *Pipa* and *Gastrotheca*. A thinned and vasculated integument such as that of the throat of a calling male toad (*Bufo*) between calls is easily distensible and might serve as the type of dorsal integument we would expect the female *Pipa* to have immediately after egg-laying. Bartlett (1896) showed that the eggs were squeezed out of the everted cloaca of the female over her back. These eggs adhering by their own capsules would form shallow pockets; the thinned integument would naturally buckle up around each egg, forming a pouch (Fig. 11). The lid (Fig. 12) to each pouch caused the earlier investigators much trouble. It has the exact histological structure of an egg-capsule (presumably the outer) and I can see no reason for its not being one. As development proceeds, that part of the egg-capsule not exposed to the

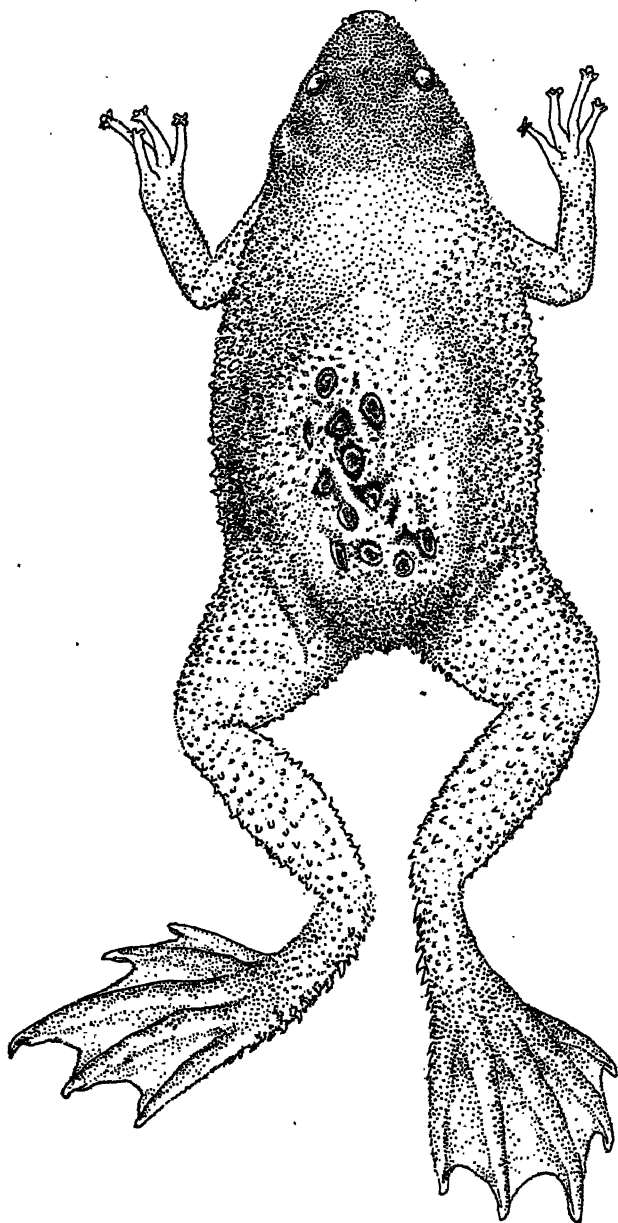


FIG. 11.—Adult female *Protolipa aspera* carrying advanced larvæ in the dermal pockets on the back.

water would thin just as do the egg-capsules of *Gastrotheca*, *Salamandra maculosa* and probably those of all species that have their eggs more or less enclosed within their bodies. In short, we have merely a scattering of eggs adhering to a vasculated integument which as a result of the pressure from the eggs has pushed up around them. That part of the egg-capsule exposed to the water swells and hardens, taking on a different appearance from that enclosed by the integument.

The conditions in *Gastrotheca* are practically the same as in *Pipa* except that before egg-laying a crescentic furrow is formed on the sacral region of the female. This may take shape very early, as Gaige (1922) has found it in young before hatching. I have seen males (of *G.*

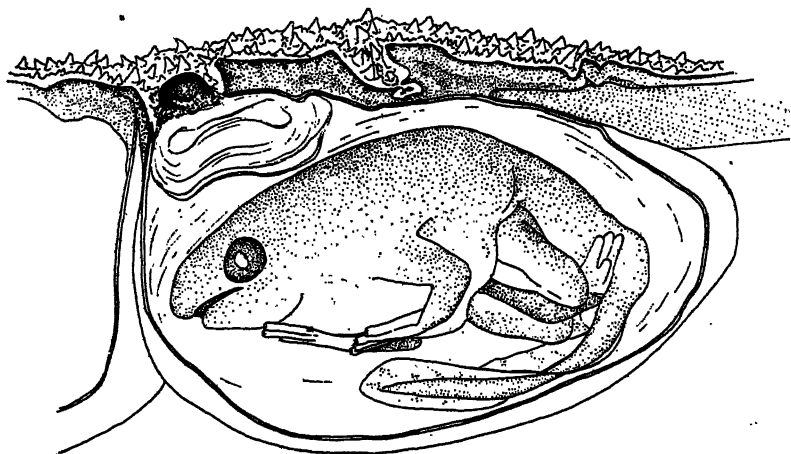


FIG. 12.—Vertical section of one of the dorsal pockets of *Protopipa aspera* showing the distention of the sack and the form of the operculum.

plumbea) that showed a slight crescent in the same region. All females of a large series of *G. monticola* which I collected have some suggestion of this pouch. It is, therefore, legitimate to assume that *Gastrotheca* differs from *Pipa* in having only a limited region of the dorsal skin thinned and vasculated before egg-laying. As the eggs are poured into the crescent, it would stretch like the throat of the male toad and a sack enclosing all the eggs within it would result. There is no histological evidence for believing that any integument reacts to the eggs in any other way than by stretching, thinning and increasing in vascularization. It is interesting to note that the detailed form of the resulting sacks should be so similar in *Protopipa* and *Pipa* and so different in *Gastrotheca*.

The various stages in the development of *Protopipa* are unknown. The

late larvæ, however, resemble those of *Pipa*. The larvæ of both *Protopipa* and *Pipist* do not hatch from the dorsal sacks until fully metamorphosed (Figs. 11-12).

PELOBATIDÆ

As in the case of the other primitive families of Salientia, the Pelobatidæ include today only a few genera. But these have undergone a greater range of adult adaptation than is found in either liopelmids or discoglossids. The larval specialization is equally great in this family, but as there are more species and genera to consider than in the preceding families, the abruptness with which the larval type may change presents itself more forcefully. It is largely this plasticity which has until recently given the impression that the mode of life history tended to obscure rather than elucidate the relationships of the forms considered.

Mention has been made of the lumbar embrace and the simple larval teeth as characterizing the primitive Salientia. The larval teeth of such very distinct, and geographically widely separated pelobatids as *Megalophrys hasseltii* and *Scaphiopus holbrookii* are remarkably similar (Fig. 13) and of a distinctive type not found in either the more primitive or the higher frogs. The number of larval teeth rows in *Scaphiopus* varies from species to species, but tadpoles of the larger species such as *S. holbrookii* agree well in both these and other larval characters with *M. hasseltii*. As in the case of all unspecialized tadpoles, however, there are in these species very few larval characters that can be seized upon as of systematic value.

The most primitive genus of pelobatids is very probably *Megalophrys* (Noble, 1924, 1926). The tadpoles of nine species of the genus are known. It has often been pointed out that these fall into two radically different groups—so different that some authors would relegate them to different genera (utilizing the name *Leptobrachium* for *hasseltii* and its allies). The first group includes *M. hasseltii*, *M. pelodytoides*, *M. intermedius*, and their allies. The larvæ are unspecialized and the adults *Rana*-like. In the second group of species, the tadpoles differ from those of the first group by having a large protusable "umbrella" or funnel-shaped mouth and a median vent (instead of dextral). For a long time the position of the vent was considered not only a good generic but even a family character in the classification of the Salientia. Today, however, we know of a number of natural genera that include some species with median and others with dextral vents, as for example, *Ceratophrys*. This character in itself is, therefore, of no great significance.

The other character which distinguishes these groups has perhaps caused more discussion than any other single tadpole feature. Today six species are known to possess this funnel mouth: *M. montana*, *M. stejnegeri*, *M. major*, *M. ligayæ*, *M. parva*, *M. robusta* and *M. boettgeri*. The funnel mouth is formed by an enormous expansion of the larval lips, a complete loss of the typical larval teeth and the modification of

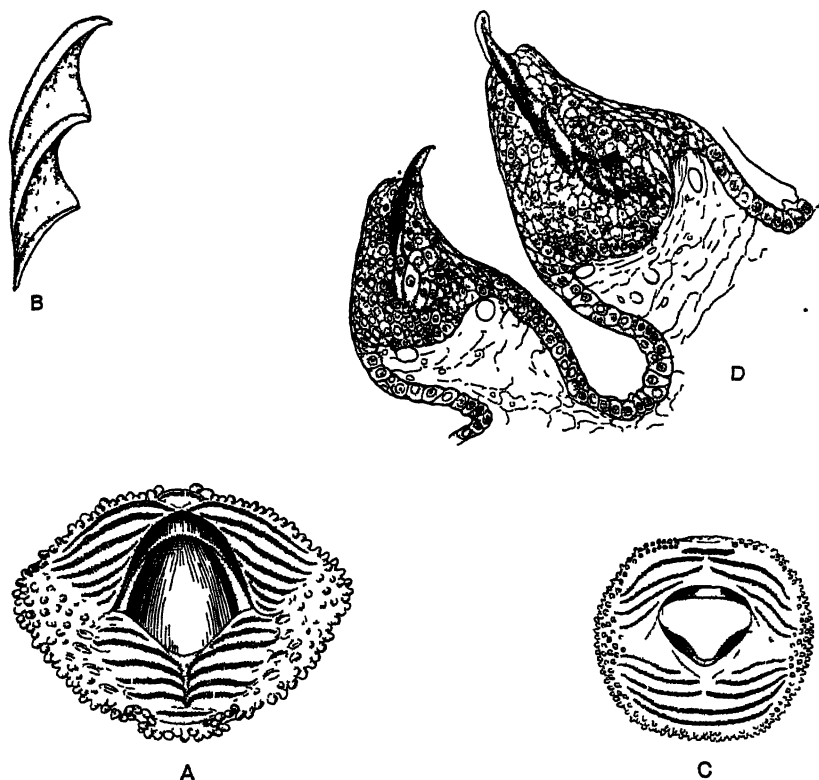


FIG. 13.—the larval buccal apparatus of the Pelobatidae: (A) buccal apparatus of *Megalophrys hasseltii*; (B) two teeth from the same specimen, $\times 360$; (C) buccal apparatus of *Scaphiopus holbrookii*; (D) sagittal section of two teeth rows of the larval *Scaphiopus holbrookii*.

both larval mandibles. All of the tadpoles thus distinguished live in mountain brooks, although they have been reported several times in quieter water. The great difficulty has been to assign a definite function to the strangely modified mouth. When folded, it has been reported to serve as a hook to prevent the tadpole from being washed downstream (Hora, 1922); when open, as a sucker (Annandale, 1912), as a rasping

organ (Van Kampen, 1909), as a float (Annandale, 1903, etc.) or as a surface feeding device (Smith, 1917, Boschma, 1922).

Smith (1917, pp. 271-272) has very definitely expressed his views as to the function of the funnel mouth in *M. montana*.

The conclusion that I came to with regard to the "funnel" was that its chief, and possibly its sole, function was to enable the creature to obtain its food, much in the same way as the membranous lip of *Microhyla achatina*. . . .

That the funnel acts as a float, and is of assistance in that way to the creature whilst feeding, is evident, but that its functions ever can be to enable its owner to float away upon flood water into safety, as has been suggested, I doubt very strongly. Certainly, at the first signs of disturbance in the water, mine in captivity invariably curled up their floats and sank to the bottom. I never saw mine use the "funnel" as a rasp, as Van Kampen has remarked, and they fed so persistently at the surface, that I imagine this to be the usual method of obtaining food.

The presence of two types of mouth within a single genus of pelobatids is not fatal to the hypothesis advocated above. Within various other genera an "umbrella mouth" may suddenly appear. In the mountain-brook tadpoles of *Phyllobates*, Dunn (1924) has showed that two species may have umbrella mouths while all other members of the genus adhere to the more typical form; similarly, in the brevipitid *Microhyla*, one species *achatina* (Fig. 30) has an enormously expanded lower lip and the others have the type of lip characteristic of the genus and of closely related genera. In *Phyllomedusa*, Lutz has recently reported an expanded lip in one species and not in the others. *Microhyla* and *Phyllomedusa* are pond dwellers and hence their expanded mouth would seem to function in surface feeding and not in the other ways which have been described for *Megalophrys*. It would seem that the expanded mouth may appear sporadically and suddenly in different groups of Salientia. It is always on a different plan of construction in different genera and on the same plan within a genus. While it is possible that the species of *Megalophrys* having umbrella-mouthed tadpoles might be grouped into a subgenus distinct from their immediate relatives, the adults of funnel-mouthed larvæ in the other families are so closely related that such grouping would be impossible.

It may be noted that both types of tadpoles of *Megalophrys* may live side by side. Annandale (1917b, p. 154) has found a tadpole of *M. montana*—or, at least, a tadpole of this type—in the same part of the stream with *M. hasseltii*. The two radically different tadpoles of *Phyllobates* dwell together (Dunn, 1924, p. 11). There is no difference in habitat between the two tadpole types of *Microhyla* or *Phyllomedusa*. Nevertheless, Dunn (1924, p. 12) concludes:

The case of *Megalophrys* seems much like that of *Phyllobates*. Adult and larva live in two different worlds, and while the general environment and habits of most species are more alike as larvæ than as adults, the reverse may be, and in these cases undoubtedly is, true.

. . . these support the precedent in time of function over form, and the possibility of apparent reversal of the biogenetic law, owing to different larval habits and similar adult habits.

These speculations do not seem to me well founded. The differences in food habits of the two types of *Megalophrys*, *Phyllobates*, *Microhyla* or *Phyllomedusa* are not known. Apparently, *M. montana* is more of a surface-feeder than *M. hasseltii*. Many other tadpoles feed at the surface, or, at least, directly under the surface. Of all larval features of Salientia, body form, teeth-row number, tail-fin, etc. (see below, under *Hyla*), this sudden appearance of an expanded mouth seems the least adaptive of all. The causes of this dimorphism of tadpoles within a genus are unknown but the data at hand would suggest that they were intrinsic rather than extrinsic.

It has often been said that the specialized larvæ of *Megalophrys* are highly adapted to life in a mountain stream. A close study, however, reveals no such adaptive features other than the slim body form and the reduced fin. The latter feature is also the chief character of mountain-brook urodeles. In all families of Salientia, mountain-brook larvæ have similar specializations. But tadpoles that rest often on the bottom (*Bufo*, *Rana*, etc.) have somewhat similar specializations, for they lack the broad fin of the "fish-like" swimming larvæ (some species of *Hyla*, *Pseudis*, etc.). Some genera have both fish-like and bottom-resting larvæ. When the variety of larval type is studied in a number of genera living under apparently similar conditions, the conviction gradually develops that all tadpoles get along with whatever structures are given them by heredity, and that some are better fitted to live in certain environments than others. Thus, only slim-bodied tadpoles can live in mountain brooks. The absence of teeth in *Megalophrys* is not a life or death character. To be sure, some mountain-brook tadpoles, like *Rana leptodactyla* and *R. semipalmata*, living in the same region as *Megalophrys* have an expanded, toothless mouth, but many others have an expanded but toothed buccal apparatus. The important point is that the mouths of the latter species are lobed and differ in detail from those of *Megalophrys*, while, on the other hand, all specialized species of *Megalophrys* have expanded mouths which are essentially alike. The detailed structure of the "umbrella mouths" differs from family to family. If a species of uncertain affinities were found to have a tadpole with larval specializations identical

with those of *Megalophrys*, the probability is great that it would prove a close ally of that genus, for extreme specializations, either larval or adult, are not likely to occur twice in exactly the same way and for the very good reason that the substratum—namely, the tadpole body—must be physiologically, and, of course, chemically, different in the respective groups.

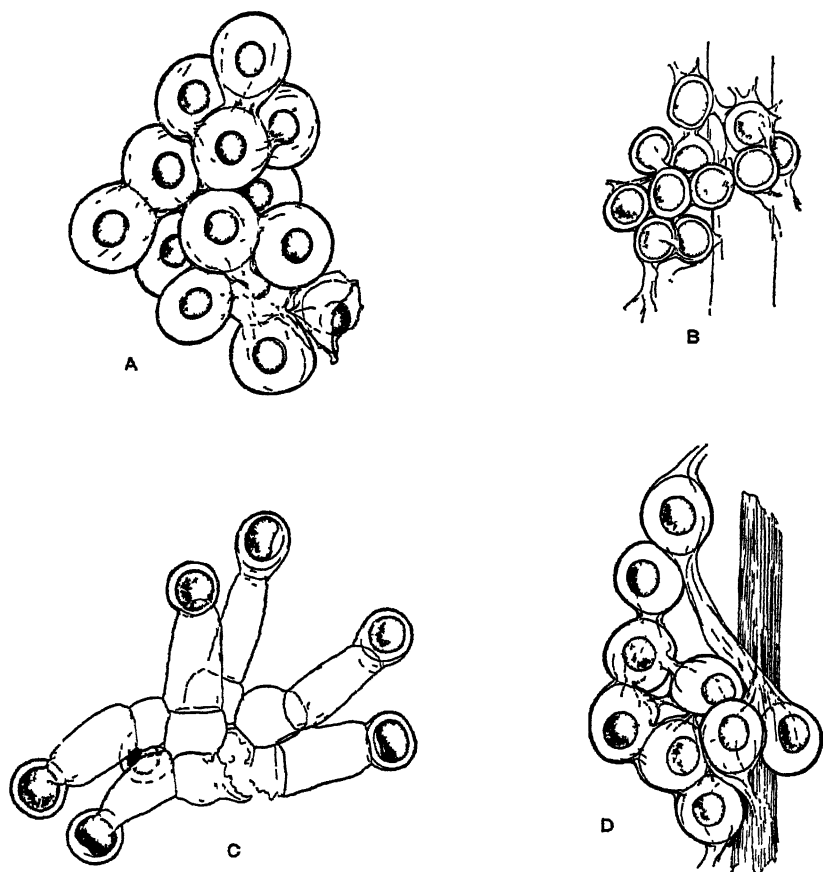


FIG. 14.—Egg clusters of certain Pelobatidæ: (A) *Scaphiopus couchii*, (B) *Pelobates fusca*; (C) *Scaphiopus hammondi*; (D) *Scaphiopus holbrookii*.

The pelobatids which inhabit the high mountains of southern Asia have arisen directly from two different stocks of *Megalophrys*, the larger genus, *Cophophryne*, from the *hasseltii* group (Noble, 1924, 1926). It is, therefore, of interest that Proctor (1922, p. 586, footnote) finds that the tadpole of *Cophophryne sikkimensis* “resembles that of *Pelobates* to

a very marked degree" for *Pelobates*, *Scaphiopus* and *M. hasseltii* have very similar larvæ.

Pelobates and *Scaphiopus* embrace the spade-foot toads of Europe and America. *Pelobates* is osteologically more specialized than *Scaphiopus*, but the two are very closely allied and should not be placed in separate families as some American workers insist. Their life histories like their structure are similar. Both breed in temporary pools after heavy rains. The egg mass is rope-like and attached to water weeds. Two egg-capsules are present in each (in addition to the vitelline membrane), but the egg-capsule form is extremely variable in the different species (Fig. 14). Other differences appear in the number of bunches in which the egg rope is laid, in the number of rows of larval teeth, the extent of the gills (Fig. 15) and in the exact form of the larvæ (Fig. 16).

Many early larval differences are not so important as they may seem. *Scaphiopus holbrookii* has a shorter intra-capsular development than any species in America. This lasts for from two to three days. It will be noticed from Fig. 16a that the larva hatches before the gills are formed. Many other Salientia hatch in an immature condition. Within a single genus we may find one species hatching at a much earlier ontogenetic stage than another. This early hatching is dependent on a precocial development of the frontal gland. Sections of the early larva show that this gland in *Scaphiopus holbrookii* is not restricted to a stripe, but extends forward over the snout (Noble, 1926 b). In any genus the difference between the tadpoles of two species during the early larval stages is usually dependent on the stage of development reached before the hatching process is initiated. Such a difference is very conspicuous in eastern America, where *Rana pipiens* hatches when only 4 mm. in length. It has no external gills and possesses the merest rudiment of a tail-bud (1 mm. long). These rudimentary larvæ do not react to tactile stimuli. *R. sylvatica*, on the other hand, has larger eggs. Its tadpoles on hatching measure about 7.5 mm. The tail is 3.5 mm. in length and has a distinct fin. Gills are present. The tadpole reacts violently to tactile stimuli. There is abundant evidence that change in yolk size has occurred often and suddenly in the Salientia. It has been difficult, therefore, to distinguish in the early stages of some related species very much that is similar. The apparently more superficial characters, such as method of oviposition, form of the egg-capsules, structure of the mature larva, would seem to guide us more surely in our general comparisons. Of more importance still is the presence of specialized larval organs of similar character in two groups.

Before concluding our discussion of the Pelobatidæ, some mention should be made of the Sechelle Island forms *Sooglossus* and *Nesomantis*, which it has recently been shown, belong to this family, although not closely related to any other genera. The first is known from the work of Brauer (1898) to have a very distinctive life history. The eggs are

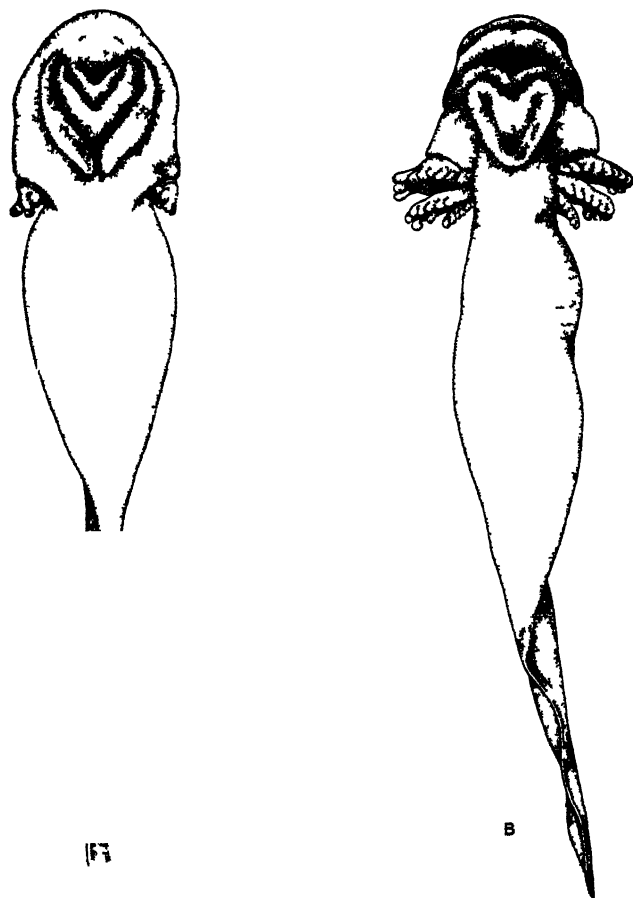


FIG. 15.—The larvæ of *Pelobates* and *Scaphiopus* a day after hatching compared, ventral aspect, (A) *Pelobates fuscus*, (B) *Scaphiopus holbrooki*.

laid on land, and the tadpoles are carried about on the back of the male parent during their entire larval life. These larvæ are peculiar in that they have no internal gills or spiracle. Thus, both larvæ and adult are structurally very distinct from their nearest relatives.

BUFOŒIDÆ

The toads Bufonidæ include such a large number of genera of such diverse specializations that the mutual relationships of many of them have been for a long time in dispute. Here, therefore developmental data might be expected to throw some light, for the life histories of a number are distinctively modified.

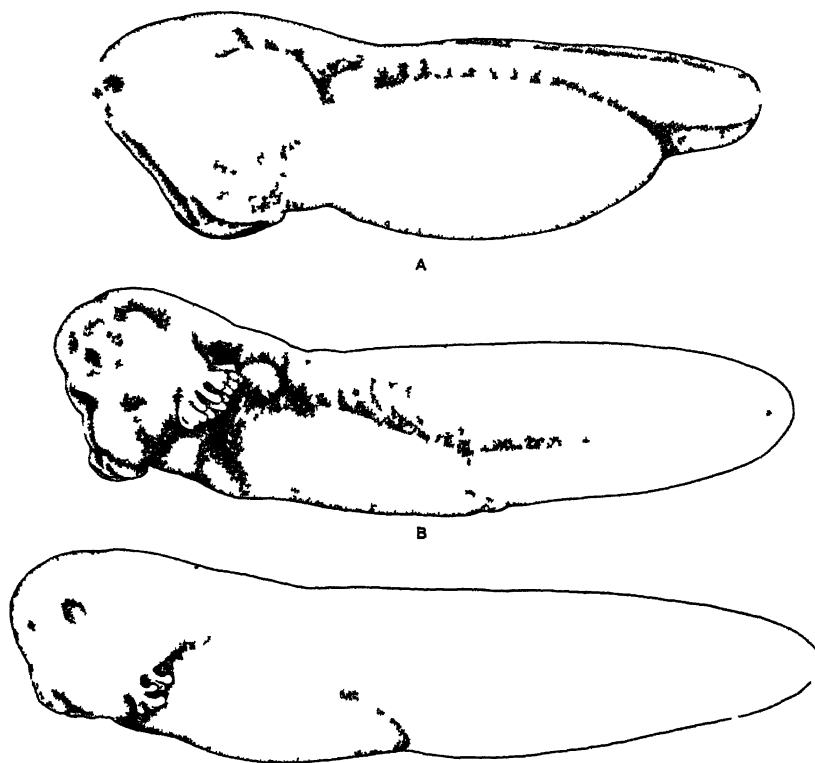


FIG. 16.—The early larvae of *Pelobates* and *Scaphiopus* compared lateral aspect (A) *Scaphiopus holbrooki*, at hatching (B) same a day older (C) *Pelobates fusius*, same stage

The greater number of the primitive genera of Bufonidæ, however, lay their eggs in the water and the larvae pass through the familiar cycle of our common frogs. Differences will be found in the details of development. These have been pointed out by Harrison (1922) for certain Australian species, and by Budgett (1899), Fernández (1921), and others for South American forms. It is difficult to recognize generic

characters in the tadpoles of these species. The famous paradox frog, *Pseudis paradox*, and its relative, *P. mantidactyla*, have back-finned tadpoles of the "pond type," while the majority of the species have larvæ of the polliwog type. The "pond type" has a broad tail and back fin. It is a dodger, similar to the deep-bodied sunfish or to the pond urodele larvæ. The polliwog type is a bottom dweller and is unable to swim gracefully in fish fashion, but either wriggles along the bottom or dashes madly through the weed to escape its enemies. As noted above, these primary types of tadpoles appear many times in different families of frogs.

One of the less specialized bufonid genera may be mentioned in some detail because of the differences of form exhibited by its larvæ. Our knowledge of the life history of this genus, *Ceratophrys*, is based upon the work of Fernández (1921) and Miranda Ribeiro (1923). The latter found the tadpoles of *C. boiei* and *C. dorsata*. The first species did not show any important structural difference from such typical bufonid tadpoles as *Leptodactylus ocellatus* other than that the digits were slightly thicker, ending in an indistinct dilation, and the toes were joined by a narrow web. The tadpole of *C. dorsata* exhibited a similar web, but had narrow digits and no incipient pads. The chief difference was to be seen in the mouth structures. The mouth of the latter species was large, directed forward and armed with many rows of teeth as well as pronounced mandibles. Miranda Ribeiro (1920) had previously placed *C. dorsata* and *C. boiei* in different genera on the basis of a few very superficial characters in the adult. He thought that these larval differences confirmed this taxonomic arrangement:

The immediate conclusion to which we are led is that *Stombus* proceeds from the *Hyla* branch, whereas *Ceratophrys* derives from *Rana*—or what is equivalent—that we are still far from an effective natural classification when we come to consider those that are up to this day known.

Fernández (1921) has shown that the tadpole of *C. ornata* is very similar to that of *C. dorsata*, while that of *C. americana*, which Miranda Ribeiro would place in still another genus, does not differ essentially from that of *C. boiei*. The webbing of the larval toes is no indication of hylid ancestry. We shall see that several species of brevipitids may exhibit such a webbing only while in the larval state. Some recently metamorphosed bufonids (*Leptodactylus lineatus*, etc.) may have broader toes and terminal expansions than the adult. The large mouth of two species of *Ceratophrys* is correlated with a cannibalistic diet. A similar diet with somewhat similar modifications occurs here and there in dif-

ferent species of *Rana*. *R. rugulosa* and *R. tigerina* have cannibalistic larvæ, and the enormous mandibles of the tadpole of *R. corrugata* suggests the same tendency in this species. None of these ranas have mouth parts exactly similar to *Ceratophrys* but none may be so cannibalistic. The size of the mouth and the number of teeth rows in larvæ of related species may be very different in closely related forms (Plate IX).

In other cases such as in the hylas of Santo Domingo the great increase in teeth rows does not form a basis for generic distinction nor should it in *Ceratophrys*, even though the functional significance of the increase may be different in *Ceratophrys* and in *Hyla*. Both *Hyla* and *Ceratophrys* include some species with unspecialized tadpoles and others with larvæ highly adapted to certain functions.

Miranda Ribeiro (1923) has described the carnivorous habits of the tadpoles of *C. dorsata*. This tadpole is of the "polliwog type." Its short tail crest would necessitate its lying in wait on the bottom or wriggling slowly about until some luckless tadpole might come in its path, when it could make a short dash for the prey. In a word, it is a plunging, not a dodging tadpole. In correlation with this body-form and habit its lungs are short, measuring only 6.5 mm. in a specimen that has a head and body (exclusive of tail) length of 27 mm. Through the kindness of Dr. Miranda Ribeiro, I have had the privilege of dissecting one specimen of this species. This specimen, the head and body length of which I have just mentioned, measured 68 mm. in total length. Its stomach and intestine contained the following food:

- (1) *Hyla* (?) tadpole entire, 15 mm. total length.
- (2) A tadpole head in one piece, 9 x 6 mm.
- (3) " " " " " " 5 x 4.5 mm.
- (4) " " " " " " 8 x 6 "
- (5) " " " and body in one piece, 9 x 7 mm.
- (6) " " " " " " " " 10 x 6.5 mm.
- (7) " " " " " and tail in one piece, 11 x 6 mm.
- (8) " " " " " " " " " 11 x 8 mm.
- (9) A mass of tadpole intestines.
- (10) About fifty Ostracods or shelled Crustacea, each measuring 1 mm. in length.
- (11) Some unidentifiable remains.

It is clear from this data that the tadpole of *C. dorsata* feeds chiefly, but not exclusively, on tadpoles, and that in seizing its brethren it usually bites them in half and swallows each half in a single piece. No other carnivorous tadpole is known to take such large mouthfuls, and no

other species has its mouth parts so well adapted for a carnivorous habit as *Ceratophrys dorsata*. Nevertheless, no structural changes have accomplished this adaptation, which may be considered highly distinctive. Other tadpoles having very different habits have developed large mouths, spike-like larval teeth and digital webs. In short, it is only when the larval modifications of one species have been compared with all the other known larval modifications that the value of these characters as indicators of relationship can be judged.

Where both the breeding habits and larval modifications are specialized and identical in two species living in the same region, it is a fair assumption that the species are related. Thus, I suggested (Noble, 1925) that *Hylodes petropolitanus* and *Borborocoetes miliaris* must be closely related, for they are the only two species of Amphibia that have greatly flattened larvæ (Fig. 6 B) adapted to scoot over the water trickles which barely cover the rocks. Both species live near Rio de Janeiro and an anatomical analysis has confirmed the close affinity of the two species which I have provisionally referred to *Borborocoetes*. The latter genus includes many species of frogs in southwestern South America. The larvæ of two of the latter, *B. grayi* and *B. taeniatus*, are known to be very different from the Rio tadpoles. They agree closely with the larvæ of *Calyptocephalus gayi*, *Telmatobius haushali* and *T. culeus*, to which they are undoubtedly closely allied. Thus, it would seem that the eastern species of *Borborocoetes* had undergone a rapid larval specialization of their own, while the adult structure of these forms remained true to type.

The bufonids were primitively a family of toothed toads very similar to their pelobatid progenitors. But here and there throughout the world different stocks have lost their maxillary teeth. Such genera were, until recently, placed in a family distinct from their toothed relatives. The resulting artificial assemblage represents a certain level of organization, but not one which can be used in discussions of distribution. Thus, the classification adapted in this paper seems of more general use. It is interesting to note that the life history data so far as known supports the grouping used here. The Australian *Pseudophryne* and *Crinia* have such similar life histories that Harrison (1922) concludes that they ought not to be separated into distinct families. Nevertheless, within each genus considerable variation occurs in egg size and in the place of egg-laying. In both genera one or more species lay their eggs on land, while others place them in the water. Thus, it may be that the closest affinities lie either between the terrestrial species or between the aquatic species of the two genera rather than between the members of any one genus. In that case the various species of *Pseudophryne* have

arisen from different species of *Crinia*. Such a polyphyletic origin is true of many genera of frogs, but where all the species have arisen from the same group in the same region, the derived genus is usually considered a "natural" assemblage (Abel, 1909).

It may be noted that the terrestrial larvæ of *Pseudophryne* and *Crinia* are unlike those of other bufonids. Development proceeds to the limb-bud stage and then remains stationary for months until a rain releases the tadpoles from their capsules. The larvæ exhibit only rudimentary external gills at an early stage. In the delayed terrestrial development of these forms there is a reminiscence of the development of the marbled salamander, *Ambystoma opacum*, which also demands an excess of moisture for development to proceed. Further, the hatched larvæ of both agree closely with the larvæ of their pond relatives.

The two large burrowing toads of Australia, *Philocryphus australiacus* and *Heleioporus albopunctatus*, are closely related structurally. They both lay their eggs on land in burrows. The eggs are of large size and covered with a frothy outer envelope. The details of development are known only for the latter (Dakin, 1920). Fletcher (1889) remarks that the external gills of the encapsuled larva of the former are large, but does not state how large. As he draws a comparison between *Philocryphus* and *Pseudophryne*, he probably means larger than *Pseudophryne*. So far as known, the life histories of *Philocryphus* and *Heleioporus* are very similar.

All of the bufonids of Australia are singularly unspecialized when compared with South American forms. The vertebræ frequently retain a remnant of the notochord. The sternum is usually cartilaginous, the terminal phalanges are simple or slightly expanded. There is no grotesque or even arboreal species. Similarly, their life histories are unspecialized. Although some species lay large-yolked eggs on land, the larvæ never possess peculiar breathing organs. No species skips over the larval stage entirely. In short, while there is a variation in egg size in these bufonids just as in all families of frogs, both larvæ and adults remain unspecialized.

One pair of South American genera is of special interest because their life history data has been used to confirm their mutual relationships. These genera, *Paludicola* and *Eupemphix*, had been until recently relegated to separate families. Fortunately, their life histories are well known, thanks to the researches of Budgett (1899), Bles (1907) and Fernández (1921) on the former, and the work of Breder and Chapin in Panama on the latter. The salient features in these life histories may be briefly outlined.

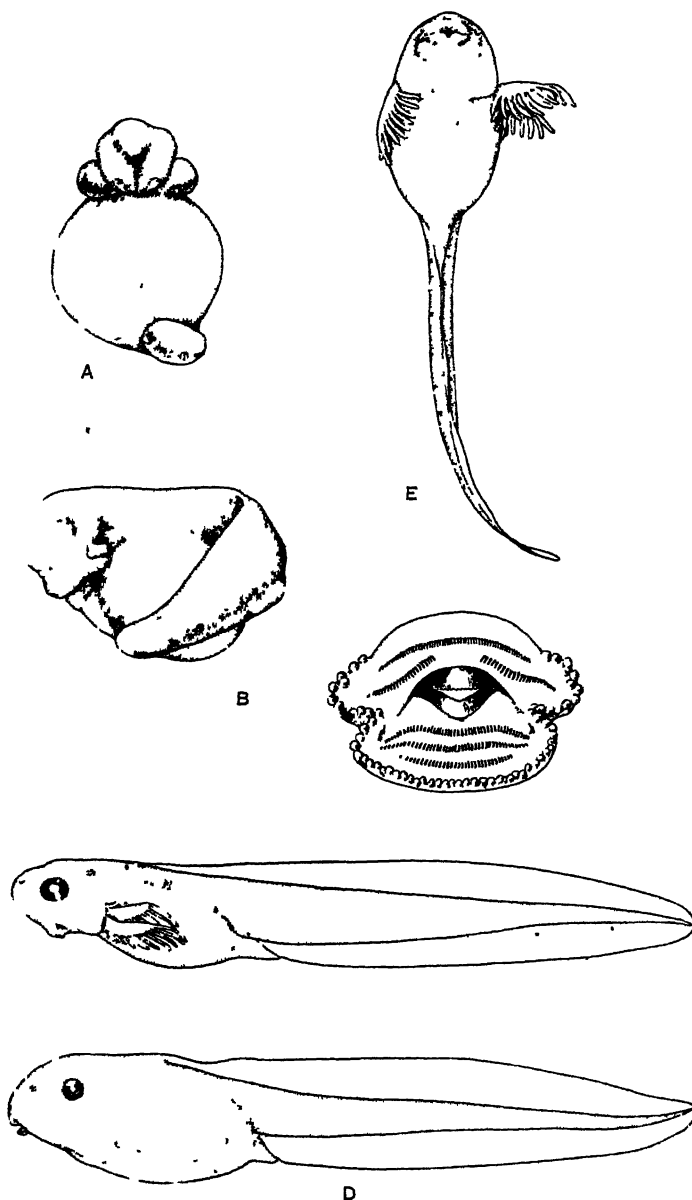


FIG. 17.—The development of *Eupemphix pustulosus* (A) ventral aspect of encapsuled larva showing the early form of the adhesive organ; (B) lateral aspect of a slightly older larva still within the egg capsule; (C) larva at hatching; (D) mature larva; (E) larva at time of hatching, viewed from below; (F) buccal apparatus of the mature larva.

Paludicola fusco-maculata lays its eggs in a foamy mass which floats on the surface of the water. The eggs are small, only 1 mm. in diameter (exclusive of capsules). Fernández (1921) states that the aveolar structure of the foam is very small. The egg masses are always laid on the borders of lakes, where they are frequently attached to water plants. Fernández never found the egg masses guarded by parent frogs. The eggs are numerous (more than a thousand), pigmentless and very difficult to see in the white foam. The development of *P. fusco-maculata* has been described and figured by Bles (1907). His plates of the different stages may well stand as "Normentafeln" of the ontogeny of a South American toothed bufonid.

The species of *Eupemphix* which both Mr. Breder and Dr. Chapin have studied, is the wide-spread *pustulosus*. It has the peculiar shoulder girdle characteristic of the genus and of *Paludicola*. Breder made his observations in Darien, Panama, during February, March and April, 1924. Most of his breeding pairs he found during the second and third

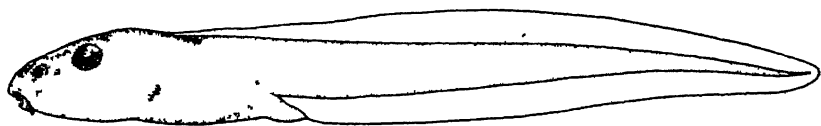


FIG. 18.—Young larva of *Leptodactylus albilabris*.

week of March. *E. pustulosus* lays its eggs in a foamy mass which floats so lightly on the water that it does not break the surface film. No less than thirty-six nests were studied critically by Breder. The nests were usually at the water's edge, generally floating but adhering to any adjacent object. The few "nests" that were not in contact with the water had probably been left stranded as the water in the pool receded during a drought. Sometimes the "nests" were partly and, rarely, completely hidden by leaves. The eggs developed normally whether or not the mass was in contact with the water. Dr. Chapin found *E. pustulosus* breeding at Tapia, C. Z., August 7, 1923, in circular basins of cement placed around the bases of trees to protect them from leaf-cutting ants and kept filled by rain water. The egg masses were laid on the edges of this basin exactly as in the case when larger bodies of water were utilized. Other egg masses were found in small stagnant pools near by and even in hoof marks which had become filled with water.

The eggs of *E. pustulosus* are practically identical with those of *P. fusco-maculata*, being only 1.4 mm. in diameter, unpigmented and laid in large numbers. Development, however, is slower than in the latter species and many details which Budgett tells us are "blurred and, as it

were, hurried over" in *P. fusco-maculata* are accentuated in *E. pustulosus*. In both species the yolk is small, but obviously dense, for the embryo soon curves around it instead of incorporating it at once into the body as in our common frogs and toads (Fig. 17). The adhesive organs, which Bles found to arise separately in *Paludicola*, differentiate in *Eupemphix* from a crescent (Fig. 17 A) as in less specialized frogs (*Scaphiopus*, etc.). The external gills, which remain small in the first genus, soon develop extraordinary proportions in the latter (Fig. 17). The nasal pits differentiate in the latter at the apex of the head and are not visible from the ventral surface as in the case of the former. In short, practically every larval feature other than general body form differs in *Paludicola* and *Eupemphix* during the early stages.

Here again as in the pelobatids and ranids mentioned above the early larval stages may show great differences when the other life history features are very similar. In the case of *Eupemphix* and *Paludicola* the differences, however, are not due merely to the different stage at which the frontal organ cells begin to secrete their liquifying fluids, a change in the growth rate of the whole or a part of the *Eupemphix* embryo must have occurred to produce the large gills (Fig. 17 B) and other distinctive features of the early larva. Nevertheless, the place of egg deposition, the form of the egg mass and egg-capsules, the structure of the mature larvæ and the general breeding habits are much alike and confirm our conclusion that the genera are closely related.

Leptodactylus is closely related to *Paludicola* but perhaps more closely to *Pleurodema*. Although the life history of *Pleurodema* is unknown, certain comparisons may be made between *Leptodactylus* and *Paludicola*. All species of *Leptodactylus* make froth nests. These are probably always in contact with water. Sometimes the nests appear to be on dry land. Thus Breder found many nests of *Leptodactylus pentadactylus* in dry hollows. But when the nest was pushed to one side, a small amount of water was in most instances found directly beneath the egg mass. In a few cases there was not water beneath the eggs but, as the water was near at hand, it may be assumed that the eggs were laid as usual on the water and that later the water partly dried up and receded before the larvæ hatched out. *Leptodactylus pentadactylus* lays its eggs always in the vicinity of small bodies of water, never on the edges of ponds or large pools. A freshly laid egg mass always exhibits a depression in the center, suggesting that the female lays her eggs in a circle about her, as in the case of *Leptodactylus ocellatus*. Unlike the female of *L. ocellatus*, which, as Fernández (1921) has shown, usually stays with the eggs, the female of *L. pentadactylus* never abides there. The details of development need

not be mentioned here. It may, however, be noted in passing that the young tadpoles of many, perhaps all, species of *Leptodactylus* are slimmer than the mature larvæ (Fig. 18). In this they agree with *Eupemphix* and *Paludicola* in which a decided change in form occurs as larval development proceeds.

One peculiarity of the eggs of *Leptodactylus* is the great variability of pigmentation. *L. orellatus* lays its eggs on the surface of pools. The eggs are pigmented. *L. gracilis* deposits its eggs in holes near the water's edge. They are unpigmented. So far we find an agreement with the often repeated statement that eggs exposed to the light are pigmented and those that are hidden are without pigment. But *L. pentadactylus* has strongly pigmented eggs. *Paludicola cinerea* has pigmented and *P. fuscomaculata* pigmentless eggs. In a single bunch of *Leptodactylus albilabris* eggs, all in the late gastrula stage (neural tube just formed), some eggs

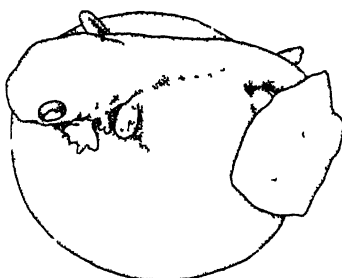


FIG. 19.—Early larva of *Eleutherodactylus inoptatus* showing the transitory gills of this species.

are nearly dark brown and others nearly yellowish white. Most are intermediate between these two extremes of color. In short, while it is possible that many eggs laid in crevices, under rocks, or other concealed places, fail to develop pigment because of the absence of light, the reverse is by no means true. A few years ago I collected some eggs of *Scaphiopus holbrookii* which were pure white. No pigment developed until the larvæ had large external gills. Then the pigmentation increased so rapidly that within a week these larvæ were nearly the color of larvæ from normal eggs collected at the same time. The variation in color in *Scaphiopus* was probably due to some abnormality. Storer (1925) has described a similar modification in *Triturus torosus*. That of *Leptodactylus albilabris* seems to be typical of the species.

The great range of variation which may occur in the embryo or early larval form of closely related species is well seen in the West Indian piping frogs, *Eleutherodactylus* (= *Hylodes* of authors). All species

clearly referable to this genus lay their eggs on land and these develop directly into frogs. The embryo within the egg-capsules has a greatly flattened tail, which obviously serves for respiratory purposes. No larval mouth parts are developed and in most species no external gills. Thus the embryo can hardly be described as a tadpole enclosed within the egg-capsules. It is remarkable that two West Indian species of the genus should have external gills during an early stage of their development. In *E. inoptutus* (Fig. 19), at least, these gills have the form of tiny handkerchiefs held in the middle and allowed to float freely in the intra-capsular fluid.

In *Eleutherodactylus*, as in *Eupemphix*, the later larval features and mode of life history are more diagnostic of relationships than the early larval characters. The diagnostic characters of the life history of *Eleutherodactylus* are the terrestrial mode of egg-laying, the large eggs with two or more thin resistant capsules devoid of peduncles or "foam," the absence of tadpole mouth parts, the presence of a premaxillary egg tooth and a broad highly vasculated tail. Some of these characters are found in other families which lay terrestrial eggs, but not all.

One species of bufonid referred to *Eleutherodactylus* lays its eggs, it is said, in the water, where they undergo a normal tadpole development. It is highly probable, however, that this species is not a true *Eleutherodactylus* (Noble, 1925). More information is desired in regard to this species, *Iatrus*, of Texas and also of the South American *Craspedoglossus* (= *Zuchaenus*) *sanctae catherinae*, which is closely related to *Eleutherodactylus* and has very similar terrestrial eggs. In fact, our knowledge of most bufonid life histories is very fragmentary.

The most primitive African bufonid is the South African *Heleophryne* (Noble, 1926). The tadpoles of three species of *Heleophryne* are known. They are all essentially alike and highly adapted to mountain-stream life (Hewitt, 1926). Their large suction mouths help them to cling to rocks in the current. In detailed structure these larvæ do not agree with any other mountain-stream tadpoles. Superficially they resemble the larvæ of *Asaphus*, but Hewitt (1926) has shown that the larval teeth are denticulated, an advanced character, and the mandibles are strikingly unlike those of *Asaphus*. No other African Salientia have larvæ similar to *Heleophryne* and no other African forms are closely allied to this genus (Noble, 1926).

The majority of African bufonids are toothless in the adult, unlike *Heleophryne*. The dominant genus is the true toad, *Bufo*. It is a remarkable fact that the species of *Bufo* whether in Africa, South America or India retain practically the same mode of life history. The eggs

in all species save the diminutive oak toad of Florida, *B. quercius*, are laid in strings. In the latter species they are deposited in rods (= short strings). The tadpole is always of the polliwog type, usually densely pigmented and undergoes a rapid development. *Bufo* ranges from Alaska to South Africa, and it may lay its eggs in alkali (Storer, 1925) or fresh stream waters. The environment of *Bufo* is extremely variable, but its life history is singularly constant.

One species of South African *Bufo* that has recently been described (Power, 1926) has a peculiar occipital crest. The eggs, however, are small, densely pigmented, and are laid in two strings as in the case of our common toads. The mature tadpole is also densely pigmented. Thus, even this species, *carens*, does not depart very far from the generic type.

In southern Asia there are a number of toads usually referred to *Bufo* but differing from it in their much slimmer form and longer legs. The only one of these whose life history is known in any detail is *penangensis*. It lays comparatively large pigmentless eggs (ovarian eggs 2 mm. in diameter). Its tadpole is peculiarly adapted to mountain-stream life (Fig. 20). As such specializations are otherwise unknown in *Bufo*, I have endeavored to find in the osteology of the adult evidences of its true relationships. The long and narrow prefrontals of this species in broad contact, its ossified cranial roof and especially its dilated and flattened terminal phalanges suggest affinities to *Nectophryne*. The life history of no Asiatic species of *Nectophryne* is known. *N. hosii* of Borneo, however, it has been stated (Roux, 1906), lays its eggs in strings as does *Bufo*. *Nectophryne picturata* of Sarawak, which was reported to have large unpigmented eggs (Smith, 1921, p. 199), has more recently been shown to be a *Sphenophryne*. Thus, while the life history data of *penangensis* seem to show conclusively that it is not closely related to

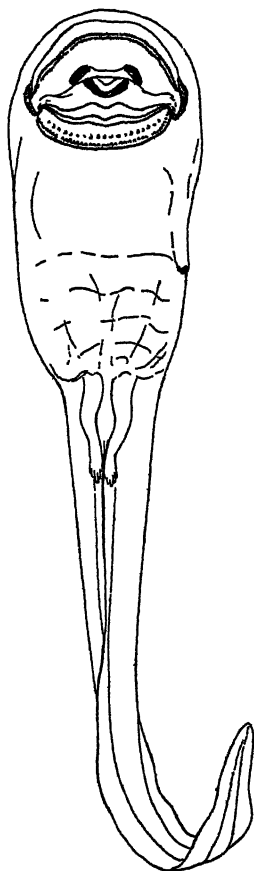


FIG. 20.—Tadpole of *Bufo penangensis*, ventral aspect.

the species of *Bufo*. lack of knowledge in regard to the species of *Nectophryne* prevents us from determining the importance of these data in showing its true affinities.

In Africa there are two groups of toads usually referred to *Nectophryne*. Members of the West African group are distinguished by their broad lamellated feet from all other species of *Nectophryne*. Boulenger (1913) has shown that *batesi* of this group lays large eggs on land, which the female "broods." The ovarian eggs of another species, *afra*, are of identical size and color. It is, therefore, not unlikely that this group has an abbreviated larval life.

The second African group I have distinguished as a separate genus, *Nectophrynoides*. The two species in this genus are the only viviparous frogs in the world. I have studied only the gravid *N. tornieri* but the conditions are probably the same in *N. vivipara*. The two oviducts are united at their caudal extremities to form a large, highly vasculated bicornuate uterus. The larvæ are remarkable for the extreme slenderness of their tails. Only a few muscular strands cover the notochordal axis of this apparently functionless appendage. The larvæ have rounded bodies but not tadpole mouth parts. In other families of Salientia (Pipidæ, Hylidæ) the larvæ may be carried in closed dermal pouches and consequently be dependent on their parental host for an oxygen supply, but the larval peculiarities of *Nectophrynoides* are not found in these species or in any other Amphibia.

N. vivipara has been considered until recently a species of *Pseudophryne*, an otherwise Australian genus. But the life history data showed that *N. vivipara* and *N. tornieri* were closely related and had no close affinity to the Australian species of the genus. Very few anatomical differences were known at the time the two species were separated off as a genus distinct from *Pseudophryne*. A more recent investigation, however, has fully confirmed the systematic arrangement suggested by the life histories. *Nectophrynoides* has solid procoelous vertebræ, while in *Pseudophryne* the vertebræ are pierced by a persistent notochord as in various other Australian bufonids (Noble, 1926). This evidence, taken together with the differences in the sacrum, omosternum and skull fully justifies the recognition of *Nectophrynoides* as a distinct genus. It is highly probable that the resemblances between the adult *N. vivipara* and the species of *Pseudophryne* is due merely to convergence. It is in cases of this sort that the life history data are particularly valuable in phylogenetic studies.

HYLIDÆ

The true tree-frogs are divided into two subfamilies, distinguished chiefly by the form of the sacrum. All species of the first group, *Gastrothecinae*,* carry their eggs in a single mass on their backs. As this habit is unique among the Amphibia, it would seem to lend additional support to this classification. Further, the larvæ of all species in the group are characterized by bell-shaped gills. In the primitive genera *Cryptobatrachus* and *Hemiphractus* the eggs are carried fully exposed on the back of the female and adhere merely by the adhesive nature of their egg-capsule. The dorsum of the parent is unmodified and the growing embryo receives neither oxygen nor nutriment from the adult. In two species of *Cryptobatrachus*, the gills, although enormously expanded, form

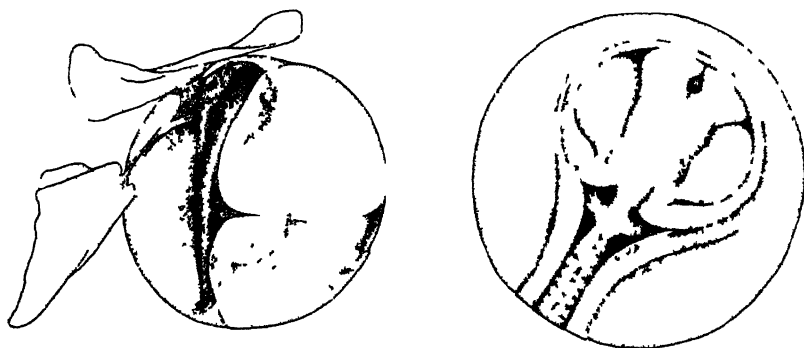


FIG. 21.—Early embryos of (A) *Cryptobatrachus elansi* and (B) *Gastrotheca monticola* showing the enormous gills of these species. In the latter, the two gills of each side have already fused to form a single sheet on either side of the neural plate.

four separate sheets of tissue. In a third species of this genus the posterior pair are lost. In *Hemiphractus*, which has specialized in a secondary armature of bone on the skull and jaws, the larval gills are modified as follows: Each pair of gill sheets on a side has fused to form a single cup or bell of vascular tissue that encloses half the embryo (Fig. 22). In *Gastrotheca* and *Amphignathodon*, which have the sacrum more expanded than is the case in the preceding genera, the egg mass is enclosed in a fold of skin or, better, a pocket which expands at every egg-laying and contracts as the larvæ are expelled until it forms a crescentic fold. A comparison has been made above between this pouch and the pouches of

* This subfamily, which I propose here for the first time, will be further defined in a later publication (Noble in MS.).

Pipa. All species of *Gastrotheca* (*marsupiata*, *monticola*, *boliviana*, *ovifera*, *plumbea* and *cornuta*) have larval gills similar to *Hemiphractus* whether the young escape as fully formed froglets or as tadpoles devoid of limb buds. I have found that in *G. monticola* the two gill rudiments of each side fuse at a very early stage (Fig. 21 B) and soon form the gill cups which have been described many times. None of the large-yolked species are known to develop the larval mouth parts that characterize the small-yolked form. This seems to be a remarkable case of breeding habits and specialized larval structures stamping a group of forms as related even though egg size and developmental details may be very different.

Amphignathodon, it has been assumed on anatomical grounds, is closely related to *Gastrotheca*. Nothing is known as to its life history

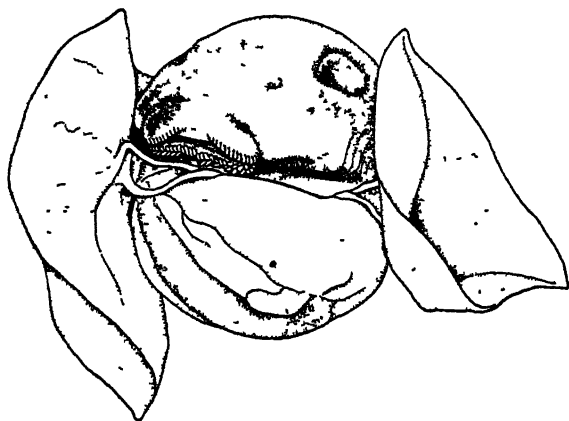


FIG. 22.—Mature larva from the sack of *Gastrotheca marsupiata* showing the "bell gills" of the genus.

other than that the female bears a dorsal pouch as in that genus. The development of true teeth in the lower jaw of this form is a remarkable case of atavism.

The second subfamily of tree frogs, *Hylinae*, grade into the *Gastrothecinae* in adult structure, but not in their modes of life history. The least specialized genus in this group is *Hyla*. The species of the genus are very numerous and spread nearly throughout the world. Nevertheless, the type of life history remains the same throughout. There is no good evidence that any species of this genus lays its eggs out of water (except certain American species to be discussed below). The tadpoles differ greatly in form (according to the strength of the current), in habits,

etc., but they never skip the larval stage. *Hyla*, like *Eleutherodactylus*, *Bufo* and most other large and well defined genera, exhibits a uniform method of life history, in spite of its wide distribution and numerous species. In the literature there are recorded certain exceptions to this rule. "*Hyla*" *evansi* and *H. goeldi* are not referable to *Hyla* but to *Cryptobatrachus* (= *Hyloscirtus*). Goeldi (1895) stated that *Hyla nebulosa* may lay its eggs out of water. There is a remarkable superficial resemblance between *Cryptobatrachus*, *Hyla* and certain species of *Eleutherodactylus*. The case of *H. nebulosa* cannot be accepted without further investigation, especially as to the structure of the adult. On the other hand, the following neotropical forms, determined by dissection to be typical *Hyla*, all lay their eggs in the water and the larvæ go through an aquatic development: *Hyla polytaenia*, *H. faber*, *H. rubra*, *H. baudini*, *H. microps*, *H. dominicensis*, *H. septentrionalis*, *H. vasta*, *H. pulchilineata* and a series of forms discussed below. Further, all species inhabiting temperate regions of the northern and southern hemisphere likewise lay their eggs in water.

In *Hyla*, as in many large genera of Salientia, the tadpoles do not conform to a single type. Those species which lay their eggs in ponds have either broad-finned tadpoles of the "sunfish type" or bottom-wriggling larvæ of the "polliwog type." The "sunfish type" has larger lungs, remains more frequently between surface and bottom and is usually a graceful swimmer. The "polliwog type" has a narrow fin restricted to the tail or only to the tail and posterior part of the body. This type is prevailingly a bottom-wiggler but may dart very rapidly in the undulatory manner characteristic of our common *Rana* polliwogs. In the eastern United States these tadpole types occur in the same pond. The tadpole of *Hyla versicolor* is a graceful swimmer, seeking the water-lily stems through which it dodges when approached, while the tadpole of the common spring peeper, *Hyla crucifer*, cannot dodge or swim in the manner of *versicolor*. The species of *Hyla* breeding in mountain brooks frequently display a remarkable correlation between larval form and current rate of the waters in which they live. In Santo Domingo I found that the tadpoles living in a certain stream called Lo Bracita were all segregated into particular parts of the stream according to their ability to withstand the current. *Hyla dominicensis* laid its eggs in stagnant pools of rain water in the forest or along the edge of the stream bank. The tadpoles were round-bodied and had the same number of rows of teeth found in some pond species (Plate IX) in the North. *Hyla vasta* laid its eggs in little basins in the gravel and stones on the edge of the pools in the mountain torrent (one observation). Six days after hatching the

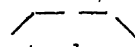
larvæ made their way out of one of the basins over wet stones into the torrent pool. As they grew older, they developed better stream lines than the tadpoles of *H. dominicensis*. They were equipped with more rows of teeth. The mouth was larger and better adapted to holding on to rocks in the stream. The tail was thicker and more muscular than that of the stagnant-pool tadpole. Finally, *Hyla heilprini* lived at much higher elevations along the stream at places where the water fell in cascades over innumerable rocks. These tadpoles had the largest mouths, the greatest number of teeth rows, the thickest tails and the best stream lines of all (Plate IX). They lived in the swiftest current and were adapted to working their way slowly over the rocks while holding on by their mouths. This series of tadpoles seemed to be an orthogenetic series progressively modified to life in a mountain stream.

Turning, however, to the adults, it became difficult to recognize these three species as forming a single closely related group of forms. *Hyla dominicensis* is a fair-sized, brown or grayish, smooth-skinned frog; *Hyla vasta* is an enormous, rough-skinned and extensively webbed form, having a very different color pattern, while *H. heilprini* is a small, smooth-skinned, pea-green species brightly variegated with gold and sky blue. It seemed, therefore, necessary to seek the immediate ancestors of these three species elsewhere and presumably in an adjacent West Indian island.

Dr. E. R. Dunn has more recently investigated the amphibian fauna of Jamaica and found four species of *Hyla* of very different sizes. The largest, *lichenata*, was rough skinned like *vasta*; further, its pupil was rhombic as in that species and quite different from that of any other West Indian or Central American species. The next to the largest species *brunnea* has always been recognized as very similar to the Dominican species of middle size. The two smallest Jamaican species agreed with *heilprini* in that they were slim and smooth-skinned. A visitor to Jamaica would very probably conclude that the three Dominican *Hyla* stocks had their representatives in that island. But Dr. Dunn worked out the life history of all the Jamaican species and found that none laid their eggs in streams or even in stagnant pond waters. All were bromeliad-dwellers, laying their eggs in the water caught between the bromeliad leaves, and their larvæ were very much alike. The tadpoles of *brunnea* and *lichenata* retain only a single row of larval teeth. The larvæ of *wilderi* and *marianæ* are without any teeth but possess a fringe of papillæ entirely around the mouth, and in the former further strengthening has resulted from a circlet of spike-like denticles around the orifice. The bromeliad habitat, the reduced dentition and the larval form of these Jamaican species were so distinctive that Dunn (1926) concluded that

they represented a natural group of species only indirectly related to the Dominican forms.

This conclusion, which to judge from all that has been discussed above, seems entirely logical, carries with it tremendous consequences. The usual characters such as rugosity, digital webbing and color that are used in the description of tree frogs would appear to be of no value as indicators of relationship, for if Dunn's conclusions are correct, a single stock that has gained access to an island can break up into a series of species, which parallel in many characters the species of an adjacent island. In the particular case in question, *rasta* and *lichenata* might be considered super-species independently evolved from *dominicensis* and *brunnea* respectively. Similarly, *wilderi* and *marianae* in Jamaica, and *heilprini* and *pulchilineata* in Santo Domingo would be juvenile or undeveloped species. The problem is not merely a matter of growth, for the specific differences are too numerous, but growth differences might be responsible for the different sizes and certain other features. The breeding habits of the two original stocks may not have been very different, for *dominicensis* uses the stagnant water in forests and *brunnea* that in bromeliads. Once, however, the original stock was established, further specialization of life history proceeded in different directions on the two islands. Today, the only good evidence of this independent evolution is to be found in the life histories of the forms considered.

The large tree frogs of South America, the *maxima* group, are distinguished from their smaller relatives, not only by their size, but by their large internal nares and  shaped vomerine teeth-rows. It is probable that they form a natural group of species within the genus *Hyla*. The life histories of only two species in this group are known. One, *faber*, inhabits eastern Brazil and the Guianas, the other, *rosenbergi*, northwestern South America and Panama. It is an interesting fact that these two species have very similar breeding habits. They are the only Amphibia that build mud basins—veritable nests—for their eggs and larvæ.

The breeding habits of these two species may be mentioned in further detail, for if Goeldi's account (1895) is correct, the part played by the sexes in the nest-building is different in the two species. Goeldi's observations were made by moonlight, and there is a strong possibility that he may have been mistaken as to the detailed movements of the breeding frogs. In the case of *H. rosenbergi* the male does all the nest-building. This was determined not by direct observation but by the discovery that, when the nests are being built, only the males are in or near them. In Panama, the nests are made in the forest along drying pools, close enough

to the edge of these rain-water or stream pools to be filled by seepage from the main body of water. Occasionally, they are constructed exactly as in the case of *H. faber* in shallow water and the walls of the circular basin or nest are built up above the surface of the water as Goeldi described for that species. On one occasion a rock crevice was utilized for a nest and a dam was thrown up across the outer end, converting the crevice into a basin. And again, a pothole was used without any mud superstructure. A study of a large series of nests which had just been built convinced Breder that the male constructs the nest by pivoting around on his pelvis and patting with the hands the earth walls which are thrown up by this movement. The shape and size of the nests is in agreement with this hypothesis. The males build these nests only at dusk or after dark. They return on successive evenings and call for a mate. The females are attracted to the nests by the call of the male.

Breder found that two broods of larvæ (in different stages of development) may be raised in one nest at the same time. Further, an old nest may be used again long after the larvæ have metamorphosed and left it. Whether the original nest builder was the paternal parent of these several broods of tadpoles could not be determined definitely, but it seemed highly probable. Breder constructed three artificial nests near the ones built by the frogs. Although other nests were later made by the frogs adjacent to the artificial ones, the latter were not utilized until the rains had practically destroyed them and until they were reduced to ill-defined depressions. The fact, however, that frogs did build nests in these depressions suggests that the males may select for nesting sites places where concavities already exist.

Thus, it is easy to understand how this nest-building habit of *rosenbergi* and *faber* might have arisen from basin-breeding habits such as are practiced by *vasta*. The eggs of *rosenbergi* and of *vasta* are pigmented; those of *rosenbergi* float in a single layer, those of *vasta* are stuck in clumps to the rocks in the bottom of the basin (at least, just before hatching). The recently hatched larvæ of the two species are both dark but by no means identical in form. The chief difference seems to be in the development of the external gills. Shortly after hatching these are enormous in *H. rosenbergi* (Fig. 23) and are apparently utilized by the larvæ to keep their hold on to the surface film exactly as in *Leptodactylus ocellatus*, according to the description of Fernández (1921). Attached to the surface film, these gills must function to the fullest extent. *H. vasta* never develops large external gills (Fig. 23), nor do the early larvæ even rise to the surface of their rock-lined nests.

Are these pronounced differences correlated with totally different environments or is it merely the hereditary material which is different? Unfortunately, no temperature readings of the water in the nests of either *H. vasta* or *H. rosenbergi* were taken. But the water in the adjacent pools could not have been of a very different temperature from that in the nest. Of six readings made in the larger streams adjacent to the

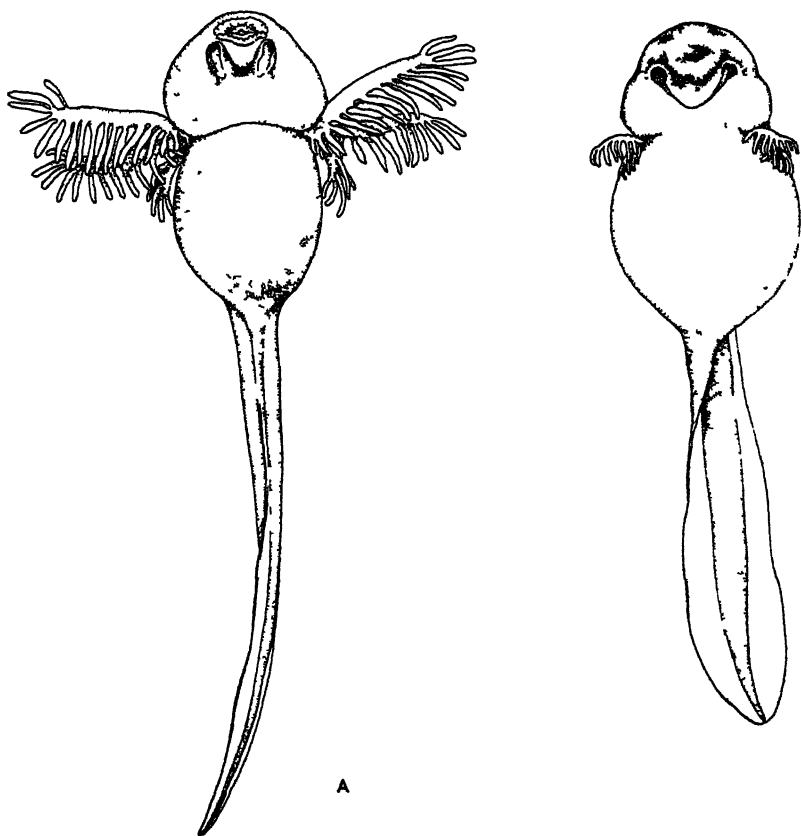


FIG. 23.—Young tadpoles of *Hyla rosenbergi* (A) and *H. vasta* (B), ventral aspect, showing enormous difference in the extent of the gills.

nests of the latter species the average temperature was 78.8° F. (max. 81.75°, min. 76.° F.). Five readings of the pool adjoining the nest of *H. vasta* were made. These averaged 74.6° F. (max. 78.°, min. 71.° F.). As the water in the nest rose and fell with the level of the pool, the temperatures taken of the pool may have been identical with that of the nest. It may be concluded, therefore, that the water temperatures in

the nests of *H. rosenbergi* were from four to five degrees higher than in the nests of *H. vasta*. This temperature difference would not account for the great structural difference in the tadpoles. *Hyla dominicensis* lays its eggs in stagnant pools that frequently are luke-warm and yet this species hatches without any external gills. At their fullest development they are only slightly longer and bushier than those of *H. vasta*.

Leptodutylus ocellatus lays its eggs in large bodies of water and Fernández attempted to account for the large external gills of this species by emphasizing the crowding to which the early larvæ are subjected. It is possible that this crowding factor may have been operative (with natural selection) in producing the large gills of the early larva of *H. rosenbergi*. The seepage in the nests of this species from adjoining bodies of water is very slow. The water within the nests is undoubtedly more stagnant than in the case of *H. vasta*. Decreased oxygen supply produced by overcrowding and stagnation may have been the chief reason for the enormous gills of the young larva. No doubt a tadpole breathing directly from the surface film with its long gills has a sufficient oxygen supply no matter how closely it may be crowded by its brothers and sisters.

The later history of the larvæ of *H. vasta* and *H. rosenbergi* are not similar, for the former leave the nest after only six days, wriggling through crannies in the wet stones in an effort to reach the torrent, there to assume rapidly the color, form and other characteristics of a mountain-stream tadpole. The tadpoles of *H. rosenbergi*, on the other hand, apparently metamorphose before leaving the nest, although nests under Breder's observation dried up before this could be determined.

There are a number of hylas which lay their eggs in small basins of stagnant water. This habit has been recorded for *Hyla* (*Hylella*) *platycephala* of Mexico and *Hyla resinificatrix* of Brazil. The latter species was originally credited (Goeldi, 1895) with remarkable powers of selecting certain gums for the construction of the nest, but later observations by Müller have shown that the species utilizes merely catch basins in the trunks of trees whether these be formed by certain insects or by accident.

It is clear from the above discussion that within the genus *Hyla* certain groups of related species have isolated themselves from the remainder of the stock by adopting certain distinctive breeding habits. New genera usually arise by a further modification of such an isolated group of species and hence the life history of a derived group might be expected to throw light on its origin. This certainly seems to hold true

for the attractive neotropical tree frogs of the genus *Phyllomedusa*. The more primitive species of the genus differ from *Hyla* only in the different proportions of the toes (Fig. 24) relative to one another. All species of the genus have a vertical pupil (as have a few hylas) and most have a green body-color and a red iris, but the only constant difference is the proportionate toe length. The specialized species have carried this disproportionate growth to an extreme. The second toe is much shorter than the first, the webs are reduced, and first finger and toe usually oppose the other digits when a twig is grasped. All species of

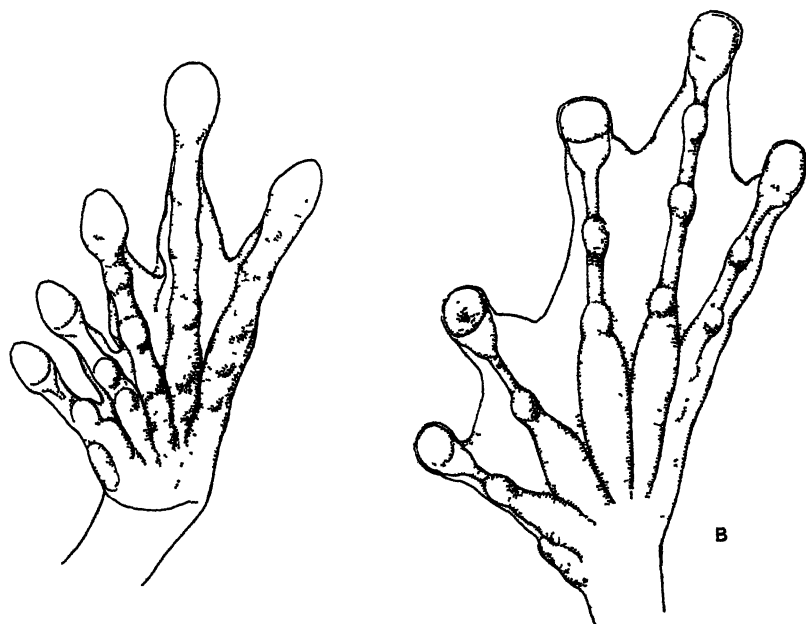


FIG 24.—Feet of *Phyllomedusa callidryas* (A) and *Hyla rosenbergi* (B) showing the different relative proportions of the first and second toes.

the genus (the least specialized forms were formerly placed in a separate genus, *Agalychnis*) lay their eggs on leaves overhanging the water. In the primitive *spurrelli*, the eggs merely adhere to the upper surface of the leaves, but in the specialized forms the parents apparently curl leaves around the egg mass. This habit would seem to resemble the nest-building of certain arboreal ranids to be discussed below. But it differs in that the parents do not beat the egg mass into a foam. Further, the larvæ as they develop exhibit a number of differences. Hence, the parallelism is confined to the habit of selecting leaves overhanging the water on which to lay their eggs.

Recently, Dunn (1924) has found that the larvæ of *Hyla uranochroa* have a red iris similar to those of most species of the genus *Phyllomedusa*. This species, when adult, is brilliant green and has much the appearance of a *Phyllomedusa*, except for its horizontal pupil. Dunn found eggs attached to leaves over the stream which he attributed to this species. The form of the nest was similar to that of *Phyllomedusa*. It would seem therefore, that one group of *Hyla* species has specialized in a red iris, a bright green color and in laying its eggs out of water on leaves over the stream. The more primitive species of this group is retained in *Hyla* because of its horizontal pupil and toe proportions. The more specialized forms add to the color characters a further hand- and foot-modification especially adapted for gripping branches. No detailed comparisons between the early larvæ of the more specialized and more primitive species have been made, but certain similarities may be expected. The later larvæ of these species, however, are of different "adaptive types." The tadpole of *H. uranochroa* is of a mountain-brook type even though its mouth is not greatly modified for holding on to rocks. Most species of *Phyllomedusa* are broad-finned pond types similar to the tadpole of *Hyla versicolor*. Further, Lutz (1924) has recently described among the pond-type larvæ one species, *P. guttata*, that has its mouth produced into a funnel to assist it in surface-feeding. Here, then, within an obviously natural group of species we find the mature tadpoles adapted to mountain-stream, to deep-pond or to plankton feeding. The mode of life history has, however, remained constant throughout the group.

There is distributed throughout tropical South America and part of Central America a group of diminutive tree frogs with flat heads, eyes directed partly forward and often with truncated digital dilations. *Centrolenella*, as the group is called, is distinguished from *Hyla* by its T-shaped terminal phalanges and its pectoral girdle without an omosternum. These differences seem important even though both terminal phalanx form and omosternum may be subject to great variation in other families. It would be impossible to judge on the basis of adult anatomy from what group of frogs *Centrolenella* evolved.

Fortunately, Breder worked out in Panama the life history of one of the species, *parabambae*, and found that it agreed essentially with that of the less specialized forms of *Phyllomedusa*. The males call with a fully inflated pouch from bushes overhanging pools of water, usually at a height of five to twenty feet above the surface. They select for a calling station the undersides of leaves, rarely the upper surfaces or axils. Their weight usually pulls the leaf down to a vertical position and the frog thus faces upward. Two clusters of eggs were found on the under-

surface of leaves overhanging the water at a place where the only frogs calling from this position were *parabambae*. It is, therefore, highly probable that these were the eggs of this species. These eggs were unpigmented, 2 mm. in diameter. The first bunch of eggs were hatching and only nine larvæ were left within the capsules. There were thirty-seven eggs in the second mass. These were well supplied with clear jelly, which enclosed the eggs in a single mass. The whole measured $25 \times 22 \times 10$ mm. One of the embryos from the second mass has been figured (Fig. 25). A comparison of this figure with that of *Phyllomedusa hypochondrialis* of a similar age (Bles, 1907) will show a remarkable similarity, especially of the long and narrow tail, the small and rounded yolk well marked off from the body of the larva and, lastly, the long and tenuous gill filaments. It is, therefore, probable that *Centrolenella* arose either from the *uranochroa* group of *Hyla* or the *spurrelli* group of *Phyllomedusa*. The former suggestion seems the more likely.

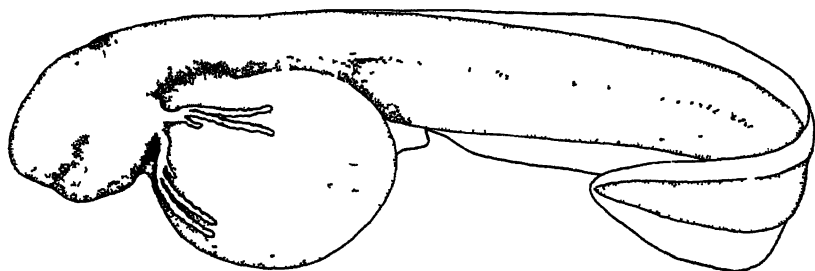


FIG 25—Encapsulated larva of *Centrolenella parabambae* showing body and gill form.

BRACHYCEPHALIDÆ

The brachycephalid toads are sharply divided into three groups which have had an independent origin from neotropical bufonids (Noble, 1926 e). This conclusion, based wholly on anatomical characters, receives an eloquent support from the life history data.

Mention has been made above of the similar breeding habits of *Phyllobates* and *Dendrobates*. These genera in previous classifications have been relegated to separate families, but for various anatomical reasons (Noble, 1922, 1926 e) must be regarded as very closely allied. All species of both genera, so far as known, have aquatic larvæ which their paternal parents carry to the pools on their backs. The tadpoles of seven species of *Phyllobates* are known—namely, *trinitatus*, *subpunctatus*, *sylvatica*, *lugubris*, *nubicola*, *latinasus* and *talamancae*. Ruthven and Gage (1915) and Dunn (1924) have described the entrance of the

tadpole-laden males into the pools and the departure of the tadpoles from their parent's back apparently never to return. Breder found in Panama a bunch of eleven small eggs attached to a dry leaf in a region where only *latinasus* was calling. Unfortunately, these eggs never developed. *Dendrobates braccatus* and *D. trivittatus* have been known for a long time to carry their larvæ in the manner of *Phyllobates*. Breder found that *D. tinctorius* had the same habit. No other Salientia have breeding habits exactly like *Dendrobates* and *Phyllobates*. Further, the various species of these genera retain their habits whether they live in tropical jungles at sea-level or on the barren slopes of the Andes at elevations of 8000 feet.

Phyllobates has been directly evolved from *Hyloxalus*, and the latter, from the bufonid, *Crossodactylus*. Unfortunately, the life history of neither genus is known but Miranda Ribeiro (1923) has given some details in regard to the related *Elosia* (*Megaelosia*) *bufonia*. It apparently has much larger tadpoles than *Phyllobates*, which would preclude carrying habits such as the Dendrobatinae show. The *Elosia* larvæ frequent mountain streams, however, as do most species of *Phyllobates*.

The second group of genera of Brachycephalidae cannot be discussed in any detail, for the life history of only the most primitive genus *Dendrophryniscus* (= *Phryniscus* of authors) is known. According to Budgett (1899), *nigricans* lays its eggs "in separate globules of jelly" in temporary pools and the "eggs and larvæ do not differ in any degree from those of *Rana*." It is probable that the most advanced genus in this subfamily, *Atelopus*, possess an aquatic larval life, for the ovarian eggs are very small and pigmented.

The third group of genera can be traced anatomically to its bufonid progenitors. *Sminthillus* has arisen from *Syrrophus* or its close relative *Eleutherodactylus*. Dunn (1926 a) has recently found that the minute *limbatus* of Cuba lays large eggs singly on land. Apparently, these undergo the usual development of *Eleutherodactylus*, although Dunn was unable to carry through the development of his specimens. The reduced number of eggs in *limbatus* seems to be correlated with the very small size of the adult. The large *Eleutherodactylus inoptatus* of Santo Domingo lays approximately twice as many eggs as the diminutive *E. abbotti* and *E. flavescens* from the same region. *Sminthillus*, it is now known, is widely distributed over South America and Parker reports large eggs as being characteristic of a species recently described by him from Brazil.

The life history of only one other genus of brachycephalids is known. This is the famous *Rhinoderma*, which carries its eggs and young in the

vocal pouches of the male. *Rhinoderma* seems osteologically very much like *Sminthillus*, but a reexamination of the "gravid" males and larvæ has revealed certain features which make it seem unlikely that the former could have evolved from the latter. The males carry a variable number of larvæ in their distended vocal pouches (Fig. 26 B). The greatest number which I have found was seventeen. The larvæ have the body form and proportions of normal aquatic larvæ. The larval teeth are present, although not cornified or pigmented (Fig. 26 D). The tail is not expanded (Fig. 26 A), but serial sections reveal that its epidermis is much thinner than that on the body. Hence, the larva probably respire primarily with its tail, as in the case of the encapsuled *Eleutherodactylus*. *Gastrotheca* tadpoles from the brood sack of the female do not show this difference in the integuments, but these larvæ are equipped with enormous external gills. The larvæ apparently remain in the sack until metamorphosis, to judge from the large series of specimens in the Field Museum which I have examined through the kindness of Mr. K. P. Schmidt. The vocal sack orifices are very large, permitting an easy egress of the metamorphosed young. Thus, the chief feature which distinguishes the development of *Rhinoderma* other than the peculiar location of the brood is the appearance of true larval teeth, which are destined never to be used. Here are "rudimentary structures" which have not the slightest use (Fig. 26 C) but structures which seem to indicate that *Rhinoderma* arose not from forms with direct development. It can, of course, be pointed out that the small-yolked species of *Gastrotheca* have redeveloped larval mouth parts, although the immediate ancestors of the stock seem to have lacked them. Thus, the immediate ancestors of *Rhinoderma* will remain uncertain until more facts are forthcoming.

In closing it may be emphasized that all brachycephalids are specialized bufonids. Hence, we would expect them to exhibit many specialized modes of life history. It is not impossible that some genera such as *Atelopus*, which are supplied with a small amount of yolk, will not exhibit the peculiarities of any of the large-yolked groups. Yolk size has been shown above to be extremely variable in the Salientia.

RANIDÆ

The true frogs, Ranidæ, unlike their derivatives, the Polypedatidæ,* are difficult to consider in this discussion because so little is known of any genus other than *Rana*. However, in *Rana*, as in certain other world-

* This family name, as used by me, embraces all the genera with intercalary cartilages, but otherwise of ranid organization.

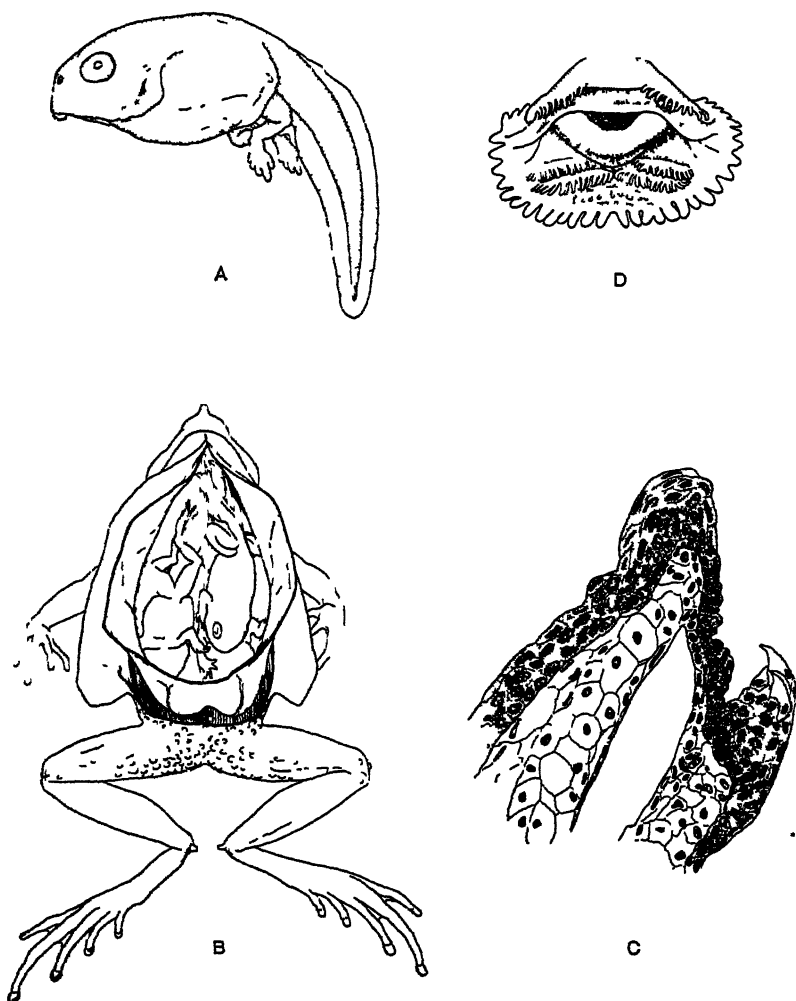


FIG. 26.—The larva of *Rhinoderma darwini*: (A) lateral aspect of mature larva; (B) partly metamorphosed larvæ within the dissected vocal pouch of the male; (C) a "useless organ," larval teeth, sagittal section, $\times 250$; (D) buccal apparatus of the mature larvæ. Note the absence of cornification.

wide genera, certain groups of species tend to develop distinctive breeding habits; and where these same habits are found in closely related genera, it is a fair inference that such genera have been derived from those species of *Rana* which had those habits, for, as noted above, life history frequently does not change when adult structures are modified but remains as a good indication of relationship.

All species of *Rana*, except one, lay their eggs in the water. Sometimes these eggs are found out of the water, where they have been left by a receding pool. No one has seen a *Rana* intentionally lay its eggs out of water, although it is probable that one other species normally does so. Nor has anyone seen a *Rana* produce foam nests even though three species of the genus have been credited with such nests. The larvæ of the various species are adapted to many different habitats. Some are mountain-brook types equipped with enormous mouths. Others are "polliwogs" and live in pools of quiet water. It has been shown above that within many families and even within a genus we may have different types of tadpoles adapted to life in streams or in the quiet water of ponds.

Of the host of *Rana* tadpoles which have been described, especially from southern Asia, there are a number which live in mountain brooks. In southern India the larva of *Rana verrucosa* frequents pools in the streams and has no special modifications. *R. beddomei* tadpoles inhabit the rocky streams of the same region and possess a much narrower tail fin than does the former; further, their teeth rows have increased by two in the upper and one in the lower lip. So far the evolution is parallel to the hylas of Santo Domingo. But the larva of *R. leptodactyla*, which is found in the pools of the hill streams, has a small downwardly directed mouth disk devoid of horny teeth. The upper lip forms a crescentic membrane which can close down over the lower. It is fringed with short pointed papillæ. The lower lip is divided into five lobes, of which two are lateral in position and much larger than the other three (Annanale, 1918). *Rana semifulmata*, which also dwells in mountain brooks, has a similar modification of the buccal apparatus. Thus, mountain-brook life does not invariably mean an increase in teeth rows. Possibly these toothless mouths can be compared with those of *Megalophrys*, at least in their sporadic occurrence, for they undoubtedly have a different function. Most mountain-brook larvæ of *Rana*, however, exhibit an increase in the number of teeth rows and a narrowing of the tail fin. In India, in addition to *beddomei*, there occurs *pleskei* (Annanale, 1917) and *curtipes* (Narayan Rao, 1914) of this type. In America the western *boylei boylei* is similarly modified (Storer, 1925).

One natural group of species often referred to *Rana* is characterized by mountain-brook larvæ equipped with a large adhesive or friction disk (Narayan Rao and Annandale, 1918) on the abdomen (Fig. 27). The only other Salientia possessing such tadpoles have been grouped together as a distinct genus *Staurois*. As shown elsewhere (Noble in MS.), there is no real difference in the anatomy of the adults and I have referred them all to *Staurois*. Thus, a larval character—namely, a peculiar

abdominal "sucker"—has pointed the way toward what I believe to be the only natural grouping of a difficult division of frogs.

It is a distinctive embryonic structure which apparently gives the best clue regarding the nearest relatives of the single land-breeding species of *Rana*. *R. opisthodon* was described long ago (Boulenger, 1886) as laying

large eggs which develop directly into frogs. The chief peculiarities of the froglet just before hatching were a series of loose folds along each side of the abdomen and an egg tooth at the tip of the snout. The folds were interpreted as respiratory structures. I have recently shown, however, that similar folds are present in the closely related *Cornufer guentheri* (Fig. 28). On sectioning (Fig. 28 D) these were found to be non-vascular and I have suggested (1925) that they are mere foldings of the somatopleure, which take place at the time the yolk is adjusted before hatching. Although these structures do not seem very fundamental, their occurrence in both *R. opisthodon* and *C. guentheri* apparently speaks for the close affinity of these forms.

Cornufer is very closely allied to *Rana*. Some species have been shifted by systematists back and forth between the genera, for the limits of the two groups are not well defined. In the ultimate analysis *Cornufer* is merely a group of East Indian and Polynesian ranas with reduced webs on their toes. It is perhaps, therefore, not surprising to find that the larval modifications of

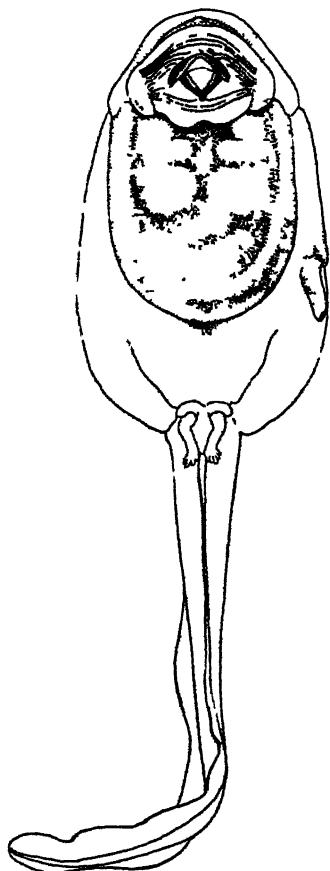


FIG. 27.—Tadpole of *Staurois latopalmatus*, ventral aspect.

Cornufer are identical to those of *R. opisthodon*. The specimens of *C. guentheri* sent me by Taylor lacked the egg teeth, but I have found in *Eleutherodactylus* that these structures are lost almost immediately after hatching. Very probably *Cornufer* froglets when within the capsules have egg teeth similar to those of *R. opisthodon*.

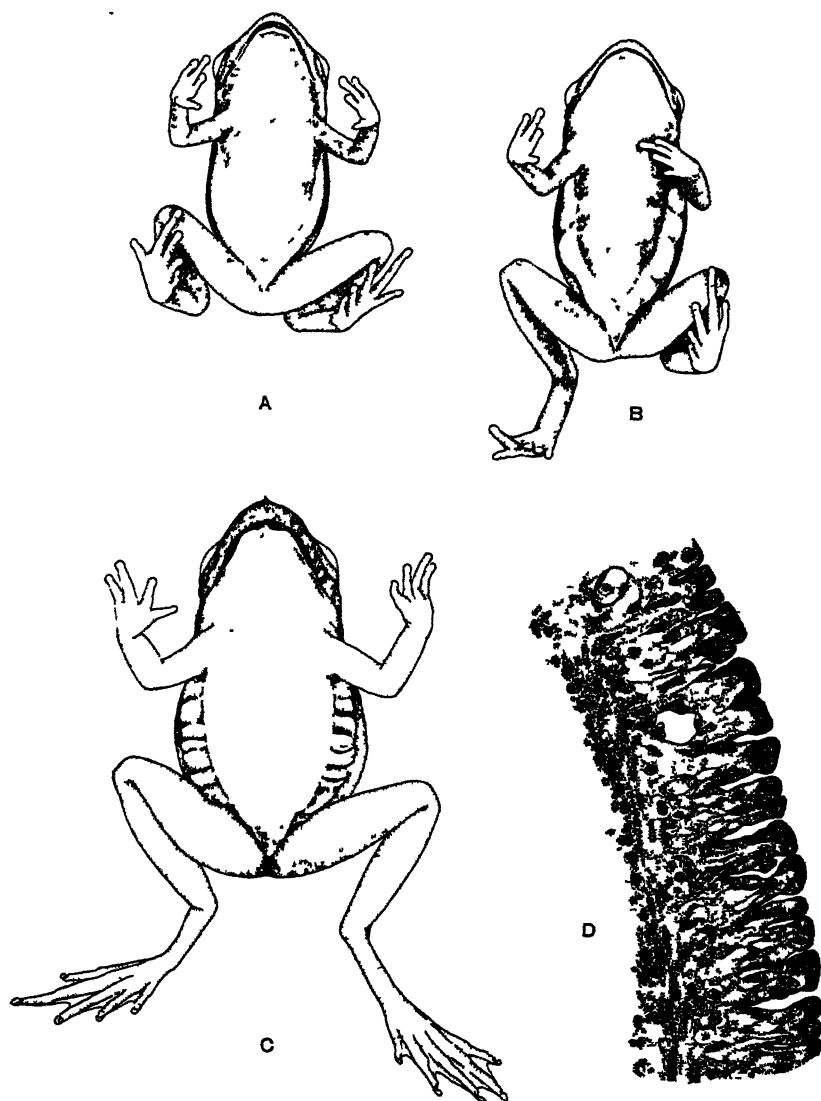


FIG. 29.—The distinctive structures of the young *Cornufer* and a related form: (A) *Cornufer guentheri*, shortly after hatching, showing the form of the lateral folds; (B) another specimen of *Cornufer guentheri* with crenulated lateral folds; (C) *Rana opisthodon*, at the moment of hatching, showing the same "respiratory" folds; (D) section of the lateral folds of the young *Cornufer guentheri*, transverse to the body axis, $\times 275$.

Cornufer very probably gave rise to a number of different groups but the life histories of none of these are known. According to a recent view

Ceratobatrachus has arisen directly from *Cornufer* and may have a similar mode of development, for, as Boulenger (1886) has pointed out, its ovarian eggs are very large.

There are a number of ranids not closely related to *Rana*. Some of these, such as *Oxyglossus*, have a very distinctive tadpole. All species of the genus *Oxyglossus* have the same peculiarities of mouth form and dorsal fin in the larva. The fact that no other batrachian has a tadpole which possesses these peculiarities speaks well for the phylogenetic isolation of the group.

The life histories of only a very few of the many genera of ranids inhabiting Africa have been studied. Some of the minute forms, such as *Phrynobatrachus* (Loveridge, 1925), lay their eggs in the water, while

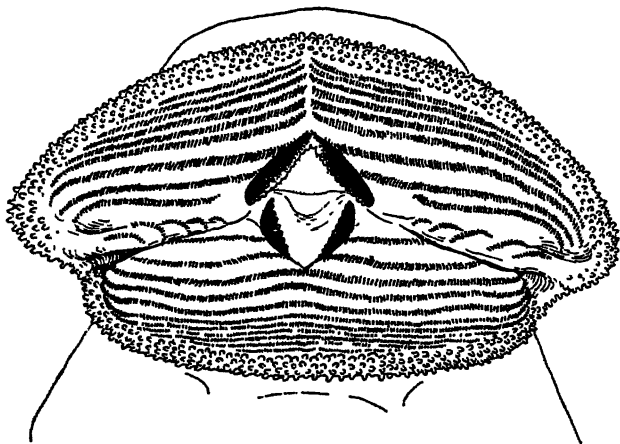


FIG. 29.—Buccal apparatus of the larval *Astylosternus robustus*.

others, such as *Arthroleptella*, deposit large eggs on land (Procter, 1925, Rose, 1926). In only one of the subfamilies of ranids peculiar to Africa is a fair proportion of the tadpoles known. But this group, *Astylosterninae*,* presents an interesting correlation between larval and adult specialization. There is a progressive ossification of the pectoral girdle and a gradual increase in the number of ventrally bent terminal phalanges in the group. Similarly, there is a progressive adaptation of the larvæ to life in mountain streams. *Nyctibates* has normal polliwog larvæ, while *Scotobleps* has the slimmer tadpoles with larger mouths and more teeth rows. Finally, in *Astylosternus* we come to the genus that has the largest mouth and the greatest number of teeth rows (Fig. 29).

* This group name, used here for the first time, will be further defined in a later publication.

Except for *Gampsosteonyx* the adult *Astylosternus* is the most modified genus in the group. The progressive adaptation of the larvæ is closely parallel to the change noted above in the Santo Domingan hylas. The chief difference lies in the adults, which are progressively changed in the ranids but apparently haphazardly so in the tree frogs.

POLYPEDATIDÆ

The diplasiocoelous tree frogs are clearly a natural group of genera and I have, therefore, separated them from their ranid progenitors as a distinct family. They parallel the Hylidæ in being an originally aboreal stock, differing from their immediate ancestors chiefly in the possession of an intercalary cartilage, or bone proximal to the terminal phalanx of each digit.

The most primitive genus is the well-known Asiatic-East Indian tree frog, *Polypedates*. The vast majority of the species in the genus lay their eggs over water and beat the egg mass with their hind legs into a foam. The tadpoles, which soon leave the foamy "nest," agree in most of their larval characters. Foam nests have been reported for *Polypedates leucomystax*, *P. reinwardti*, *P. nigropulmatus*, *P. schlegeli*, *P. pardalis*, etc. They may be placed in a great variety of situations, such as in holes in a bank, on leaves and bushes near water, on walls of a well and on vegetation overhanging the water. In this as in other genera, such as *Eleutherodactylus*, which lay their eggs on land, the nursery situation may vary enormously from species to species while the character of the egg mass remains constant.

In *Polypedates*, however, the egg mass is not always constant. Two mountain species, *reticulatus* and *everetti*, have succeeded in increasing the yolk content of their eggs until the eggs are too large to beat into a foam (Noble, 1925). No Salientia with large eggs; that is, no species which undergoes a large part of its development (or all of it) within the egg capsules, produces a foam nest. Is this not due to mechanical difficulties? At least one genus, *Alytes*, which lays eggs on land, makes incipient movements of much the same character as *Polypedates* but a foam never results. Whatever be the ultimate causes of terrestriality in these two species, they afford an interesting parallel to *Rana opisthodon*.

The tadpoles of *Polypedates* do not show the many variations of body form found in *Hyla*, *Rana*, etc. This seems to be correlated with the predilection of the parents for still water near which to build their foam nests. The tadpoles are either of the dodging type or a slight modification of this form.

Polypedates (= *Rhacophorus* of authors) has for a long time been recognized as ancestral to several other ranid genera. Perhaps the closest of these derived groups is *Philautus*. Smith (1924, p. 141) says of *P. vittatus*:

This frog is one of the few species of the genus to be found at sea level. It frequents low bushes by the sides of ponds, and makes a round frothy "nest" similar to that made by the common tree frog, *Rhacophorus leucomystax* (Gravenh.). This is attached to some bough overhanging the pool and the larvae as they hatch are washed out of it by the rain and dropping into the water below continue their development in the usual manner.

All other species of *Philautus* whose life histories have been described have been found to have similar habits. Boulenger (1912) has listed *P. horridus*. Pope has found two species of *Philautus* breeding in Hainan. Their life history is apparently similar to that of *P. vittatus* and *Rhacophorus leucomystax*, except that the nest is placed in bushes or grass and not in trees overhanging the water. Throughout southern Asia the only two genera which make froth nests out of water are *Polypedates* and *Philautus*, although others have been reported, but probably through error, and these genera are more closely related to each other than they are to any other groups.

A second genus directly derived from *Rhacophorus* is the African *Chiromantis*. It has long been known that *C. rufescens* makes froth nests and not always close to water (Noble, 1924 a, p. 237). *Chiromantis xerampelina* apparently has breeding habits similar to *C. rufescens* (Hewitt, J. and Power, J. W., 1913). *Chiromantis petersii* also builds foam nests but always over water (Loveridge, 1925). So far as known, the life history of *Chiromantis* agrees in all essential features with that of *Polypedates*.

The life histories of the African frogs most closely allied to *Chiromantis* are very imperfectly known. *Leptopelis*, which is structurally the most alike, lays unpigmented eggs of large size (Boulenger, 1906). *L. brevirostris* was incorrectly reported as carrying its eggs in its mouth and it will be a long time, no doubt, before this error is erased from the literature. *Hyperolius* has been derived from *Leptopelis* and has large ovarian eggs. The most specialized members of this group of genera—namely, *Hylambates* and *Kassina*—have small eggs (Noble, 1924). These are usually pigmented. It would seem in this instance that the small eggs of *Kassina* and *Hylambates* have been derived from the larger-yolked eggs of *Chiromantis* and *Leptopelis*. The tadpoles of certain species of these genera are known. They agree fairly well with the typical *Polypedates* tadpole. The life history of *Kassina senegalensis* has

recently been worked out by Power (1926). The eggs are small (1.5 mm. without the capsules), pigmented and laid singly or in pairs in the water. The mature tadpole is of the broad-finned *Polypedates* type. The larval teeth rows, however, are represented by only one row on the upper and two rows (one complete and one interrupted) on the lower lip.

Thus, it is clear that the habit of producing a froth nest is not found throughout this apparently natural series of genera. It would be interesting to know just where in this series of genera the habit was given up. *Kassina*, although possessing the pads (in a highly reduced form) of *Polypedates*, is, according to Power, a ground dweller. It would thus seem highly necessary that this form should have modified its life history in such a way that it could dispose of its eggs in a situation within its reach. Its tadpole, nevertheless, seems to have remained unmodified, except for the slightly reduced dentition.

The original describers of the tadpoles of *Hylambates* and *Kassina* unfortunately overlooked their most distinctive features, thus tending to retard an earlier appreciation of the thesis advocated throughout this paper. As I have shown elsewhere (Noble, 1926 c), both tadpoles are equipped with a rigid, convex upper lip and a pair of black horny plates obliquely arranged below the angles of the mouth. Such structures are not found in any other Salientia. They apparently afford us definite proof that *Kassina* and *Hylambates* are closely related even though the adult of the first is modified for terrestrial and that of the second for arboreal life.

Only a few tadpoles of the Polypedatidae have been described, and some of these incompletely so. Boulenger (1909) reports that the tadpole of *Megalizalus sechellensis* conforms to the *Polypedates* type, but has its larval teeth arranged four rows before the mouth and three behind. It would be interesting to know whether any suggestion of the distinctive larval structures of *Kassina* and *Hylambates* is found in this tadpole, for *Megalizalus* is closely related to the latter genus.

BREVICIPITIDÆ

The narrow-mouthed toads include an extremely variable group of fossorial, terrestrial and arboreal species. A study of their osteology and myology has revealed that they are ranids which have expanded their sacral diapophyses and undergone numerous modifications of skull and pectoral girdle. Formerly, the brevicipitids with maxillary teeth were placed in a distinct family, the Dyscophidæ, but a closer analysis has shown that the toothless genera have been derived from the toothed

forms in different parts of the world. The Dyscophidæ as a family cannot be separated from the Brevicipitidæ.

The life history data fully confirm this arrangement. All the genera of the two groups, excepting two genera to be discussed below, are characterized by the same distinctive type of larva (Noble, 1925). The mouth of this larva is devoid of teeth and the lips are folded in a characteristic way (Fig. 30 A). The external nares do not break through until late in larval life. The olfactory surfaces (so far as examined) are found in a rather broad-mouthed olfactory chamber protected from the contents of the buccal cavity by a tongue-shaped flap which projects forward (Fig. 30 B). Possibly this tongue controls and even directs the water into the higher portions of the olfactory chamber. The spiracle of this larva is median, unlike that of all the other higher Salientia. The toes are provided with a webbing which is usually reduced on metamorphosis. This larval type is found in such structurally diverse brevicipitids as *Calluella*, *Cacopus*, *Glyphoglossus*, *Kaloula*, *Kalophryne* and *Microhylya*. It also characterizes the American *Gastrophryne* and the African *Phrynomerus* (Noble, 1925, 1926).

There is still an additional peculiarity which will probably be found to characterize most, if not all, the true brevicipitids. The egg-capsules of *Kaloula* (Annandale, 1917 b) and *Gastrophryne* are flattened, or at least capped at one pole. Such a flattening keeps the egg in a definite position in the water. This peculiarity is not found in the egg-capsules of any other member of the Amphibia.

One species of *Microhylya*, *M. ahatina*, has a larva which differs slightly from the brevicipitid type in that the lower lip is produced and apparently functions in surface feeding (Fig. 30 D). We have already mentioned under the Pelobatidæ how, within many groups of Salientia, tadpoles suddenly appear with funnel mouths and we have failed to find any adaptive significance in such modifications. The tadpoles of *Microhylya ornata*, *M. berdmorii*, *M. pulchra*, *M. rubra* and *M. butleri* are of the typical brevicipitid type. The occurrence of a produced lower lip in *Microhylya ahatina* does not destroy our concept of a single tadpole within the genus, for this peculiarity may be considered only a variation of the typical form (see above, pp. 74-76).

Many brevicipitids have large-yolked eggs and, while it is possible that some of these have arisen suddenly from small-yolked species, as in the other families, it is equally probable that others have arisen from large-yolked forms. In other words, part of the genera having large eggs and practicing direct development may possibly represent a natural series of forms. Thus, *Oreophryne verrucosa*, which has a nearly complete

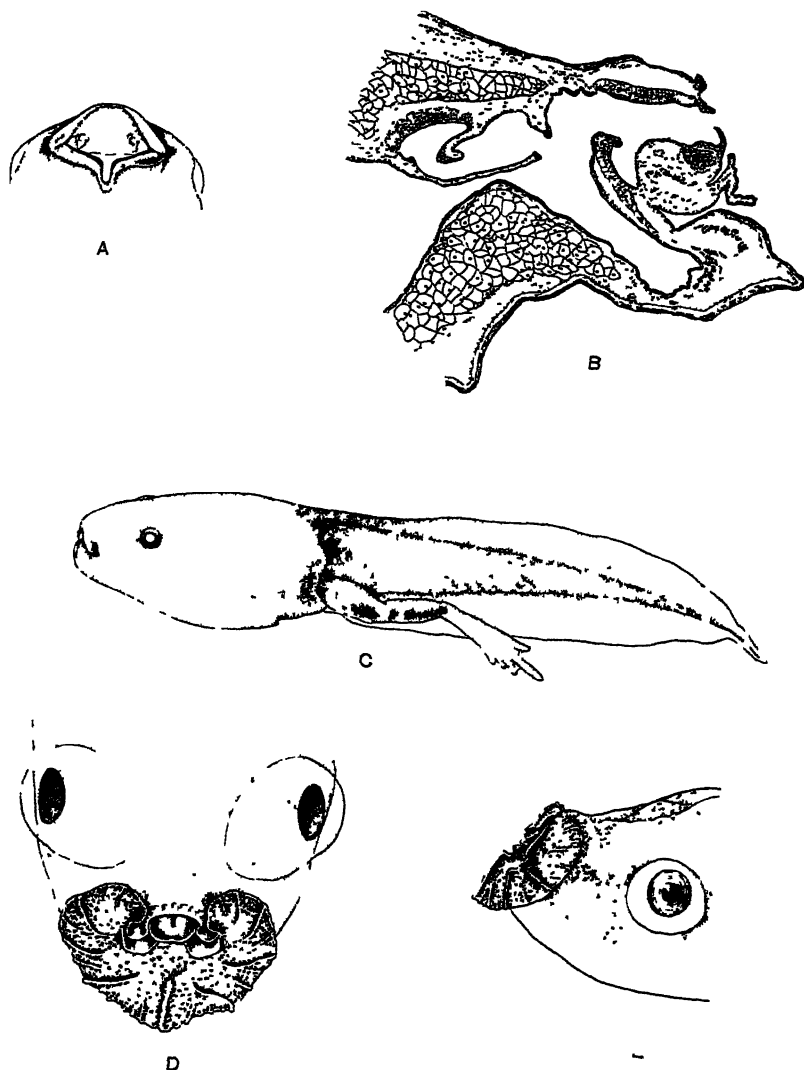


FIG. 30—The distinctive tadpole of the Brevicipitidae: (A) mouth of the mature tadpole of *Microhyla pulchra*; (B) parasagittal section of jaws of the same species, x 18; (C) mature tadpole of *Kalophrynus pleurostigma*, lateral aspect; (D) the "umbrella mouth" of *Microhyla achatina*; (E) same, lateral aspect.

The "umbrella mouth" has arisen in many different families of Salientia and has no phylogenetic significance.

shoulder girdle, lays from ten to twenty large-yolked eggs, attached to each other by a mucilaginous cord. *Mantophryne* has lost both the clavicle and procoracoid and yet the mode of life history is the same as in

Oreophryne. Both genera practice direct development. The life history of these forms has frequently been compared with that of *Eleutherodactylus*. In these comparisons little or no attention has been paid to the differences between the genera. The mucilaginous cord of *Mantophryne robustus* is not found in *Eleutherodactylus*. No egg teeth have been described in any brevicipitid. Both *Mantophryne* and *Eleutherodactylus* have a flattened tail apparently used in respiration, and seemingly the gills are lacking in the first as well as in most species of the second genus. While there are some similarities between the encapsuled larvæ of these two genera, there are also differences which demonstrate that the two groups have independently acquired the mode of direct development.

Whatever be the status of such genera as *Xenobatrachus*, *Phrynixalus*, etc., many of these New Guinean genera, which are obviously closely allied, have large ovarian eggs. *Phrynomantis biroi* lays eggs identical to those of *M. robustus* but supposedly deep in the water (Mehely, 1901). It is highly probable from Mehely's description that these were laid on land near the stream and were covered by water during a freshet. It was because of just such a freshet that Stejneger (1904) described the eggs of *Leptodactylus albilabris* as submerged when, as a matter of fact, they agree with all other eggs of the genus in being laid only in contact with water (Schmidt, 1920). No Salientia which undergo direct development are known to lay their eggs in the water. Submerged, encapsuled froglets cannot live for any great length of time within the egg-capsules. If the encapsuled larvæ are freed from their capsules, they can live for some time, possibly for all of the later stages of development, in the water. Archey (1922, p. 67) kept *Liopelma* young eleven days in water. I have kept several *Eleutherodactylus inoptatus* which were nearly ready to hatch four and one half hours under the surface of the water without death resulting. On the other hand, Boulenger (1912) could not raise the encapsuled larvæ of *Alytes* in water; nor Budgett (1899) those of *Phyllomedusa*.

One of the best cases in which the life history data have been brought forward to elucidate relationships is that of the South African brevicipitid *Cacosternum*. This little toad was originally described as a ranid but subsequent investigation revealed that its pectoral girdle was greatly reduced and its sacral diapophyses expanded as in the Brevicipitidæ. It was then considered a brevicipitid closely related to the South African *Phrynomerus*, for its pectoral girdle exhibited certain resemblances to the latter genus. Very recently the tadpole of *Cacosternum* has been made known. Instead of conforming to the brevicipitid type and agreeing with that of *Phrynomerus*, it was found to be of the ordinary ranid type.

This fact suggested that *Cacosternum* might have been directly evolved from the Ranidæ. An investigation was, therefore, made of the osteology of *Cacosternum* and its close ally, *Anhydrophyrne*. Anatomical evidence was found making it seem highly probable that both of these genera arose directly from a ranid stock (Noble, 1926 c). The problem was complicated by the fact that *Anhydrophyrne* practices direct development. The latter genus was apparently evolved directly from the ranid *Arthroleptella* (Noble, 1926 c), with which it agrees structurally except that it lacks a clavicle. *Arthroleptella* undergoes what is practically direct development (the mature larva hatches from the egg-capsule and lives a short time in moss on land before metamorphosing). The encapsuled larva agrees, so far as known, with that of *Anhydrophyrne* (Rose, 1926). The close relationship of *Anhydrophyrne* and *Arthroleptella* is apparently confirmed by the life-history data. *Cacosternum* may have been evolved from *Arthroleptella* by a sudden reduction of the yolk and a reappearance of the early larval form in development. A somewhat similar reduction of the yolk and reappearance of the larva obviously took place in the case of certain species of *Gastrotheca*. Whether or not *Cacosternum* actually arose from *Arthroleptella*, the larval features stamp it as closely related to ranids and not to other brevicipitids.

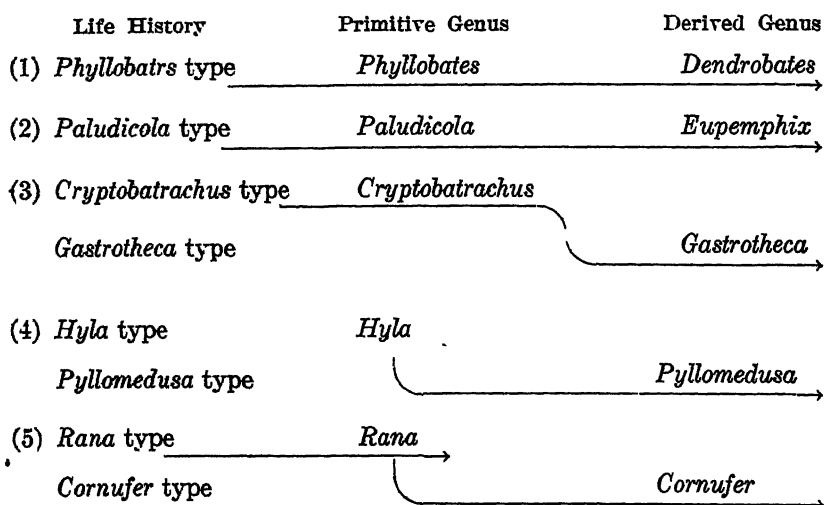
Further details in regard to the life history of the South African brevicipitid *Breviceps* (Rose, 1926) will be awaited with interest, for this genus is structurally very different from *Anhydrophyrne*. *Breviceps* undergoes its entire development within the egg-capsules.

DISCUSSION

The different types of life history exhibited by the Amphibia have been discussed above not from the usual standpoint of general similarities but from that of the taxonomic and phylogenetic relationship of the different genera. Amphibian life history, when considered in this light, is found to be not the fluctuating and easily modified process usually assumed but, on the contrary, a thing extraordinarily stable. It follows, therefore, that an identical method of life history, especially if this is a highly specialized or distinctive one, in two genera may be taken as an indicator of relationship. This general conception once established for many genera may be applied to the elucidation of the relationships of those genera whose affinities are in doubt or, at least, not generally recognized.

There is not a diagrammatic agreement between larval and adult specialization in the Amphibia. Sometimes larval specialization will occur before the adult modifications have arisen. In other words, a single natural genus may show two types of life history: its own

or more characteristic one, and another found in a derived genus. There is no reason why we should expect that life history, when it changes from one type to another, should do so exactly at that point in our phylogenetic tree where one genus branches from another. Life history type is even in these cases evidence of relationship. This statement may be represented graphically by the following diagram in which pairs of closely related genera have been selected, and the change of life history type represented by a sharp bend in the line. A detailed statement of the nature of these life history changes has been made above.



The life histories in each pair of cases (1) and (2) are specialized and very similar. This similarity in an "unusual mode" of development may be taken as further proof that the genera in each pair are related. In case (3) life history and adult modification occur at the same time but, as the larvæ are highly specialized in both stock and derived genus, we may even here use as an indicator of relationship certain characters of the specialized larva that are common to both. In other words, there would be no bend in our life history line if we were considering only the bell-shaped gills of the larva. In the last two cases, (4) and (5), the change in the mode of life history has occurred before the modification of the adult has arisen. Nevertheless, the very fact that certain species in the stock genus have the same life history specializations that are typical of the derived genus is further proof that stock and derived genus are closely related.

Egg size in the Salientia and in some Caudata is subject to great fluctuations. Species with large eggs may be derived from small-yolked species or *vice versa*. Although egg size is frequently of no generic significance, specialized larval organs may develop in correlation with this large yolk size and be retained even after a secondary reduction of the yolk (as in some species of *Gastrotheca*).

Little attention has been paid in former reviews to the detailed structure of some of the larval organs which seem to be of value in classification. Considerable attention has been given above to the different kinds of egg teeth, bell-shaped gills, larval teeth, etc., in an effort to recognize identical larval specializations in related genera. This work has brought to light many correlations which demonstrate that the larvæ as well as the adults possess generic or even larger-group characters of value in our classification. These characters are given above under the family discussion and need not be repeated here.

In the urodeles it was possible to trace the phylogenesis and modification of a particular life history type through one or even several families. This has been impossible in the Salientia because of the far greater number of genera, the vast gap in our knowledge concerning many of these and, lastly, the obviously more frequent fluctuation in egg size which has accompanied the phylogenesis of each family. The outline given above emphasizes the need for further details concerning the life history of many Amphibia and the importance of the known details in elucidating relationships that are unknown or doubtful.

CONCLUSIONS

(1) The mode of life history is a much better indicator of relationships in the Amphibiâ than is usually conceded.

(2) Homologous embryonic or larval specializations in different genera of Amphibia may be taken as evidence of the relationship of these genera. This does not apply to certain features discussed above, such as increase in egg size, increase in the number of larval teeth rows, changes in tadpole body form, etc.

(3) A very specialized mode of life history or larval structure occurring in two different Amphibia usually affords some of the best evidence that these forms are related.

(4) Habits may be more stable than many adult characters.

(5) The phylogenetic position of an amphibian is best determined by a comparison of its habits and life history, as well as its structure, with those of its relatives.

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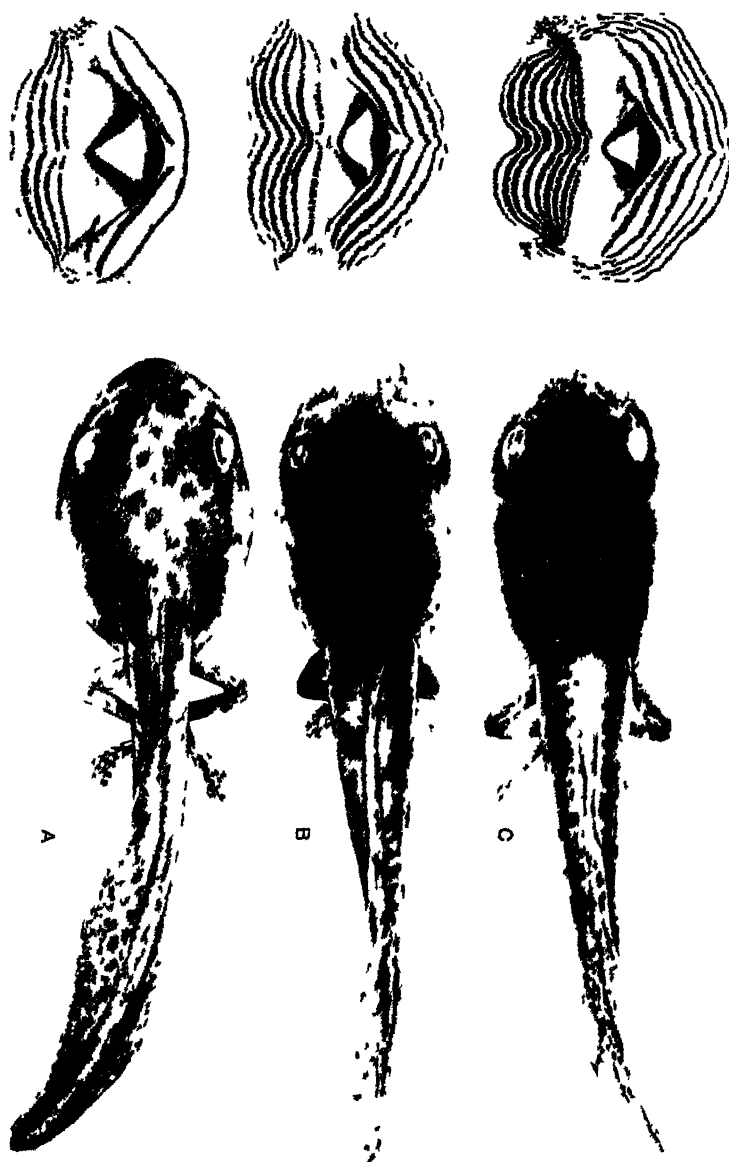
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ADAPTION IN THE *Hyla* TADPOLES OF SAN TO DOMINGO

Modification of body form and tooth row number correlated with the speed of the current
 Fig A *Hyla dominicensis* Fig B, *Hyla vasta* Fig C *Hyla hepatica*

THE INHERITANCE OF RESISTANCE OF OAT HYBRIDS TO LOOSE AND COVERED SMUT*

BY GEORGE M. REED
Brooklyn Botanic Garden

CONTENTS

	Page
Introduction	129
Descendants of crosses between Hull-less and Black Mesdag.....	130
Description of the parents.....	130
The F ₁ generation.....	131
Experimental results with the F ₁ generation.....	132
Results with <i>Ustilago Avenae</i>	133
Results with <i>Ustilago levis</i>	133
Behavior of the F ₁ generation.....	133
Results with F ₂ families descended from uninoculated F ₂ plants..	135
Results with F ₂ families descended from F ₂ plants resistant to <i>Ustilago Avenae</i>	136
Results with F ₂ families descended from F ₂ plants resistant to <i>Ustilago levis</i>	137
The F ₂ generation of crosses between Silvermine and Black Mesdag.....	139
Crosses between susceptible oat varieties.....	140
Crosses between Hull-less, susceptible to both smuts, and Early Gothland, susceptible to <i>Ustilago Avenae</i> but resistant to <i>U. levis</i>	141
Crosses between Hull-less, susceptible to both smuts, and Monarch, sus- ceptible to <i>Ustilago levis</i> but resistant to <i>U. Avenae</i>	143
Discussion	144
Summary	148
Supplementary tables A to M.....	150
Bibliography	173

INTRODUCTION

In a previous publication (31) I have described the inheritance of resistance of certain oat hybrids to loose smut (*Ustilago Avenae* (Pers.) Jens.), the data for which were obtained from a study of the descendants of a cross between the varieties Hull-less and Black Mesdag.¹ The

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former variety had consistently shown a high degree of susceptibility to loose smut in various experiments over a period of years, while the latter had been extremely resistant. The inoculation experiments described in the paper referred to were carried out with the F_2 , F_3 and F_4 generations, and the data presented indicated quite clearly that resistance to loose smut was dominant and susceptibility was recessive. Further, the facts obtained were in close accord with the interpretation that there was a single factor difference between the two parents, thus giving a simple mono-hybrid ratio of three resistant to one susceptible.

The present paper gives the results with additional crosses between these two varieties—Hull-less (Seed No. 30) and Black Mesdag (Seed No. 70)—and, in addition, crosses involving other varieties of oats are included. Further, the behavior of the descendants of these hybrids to both loose (*Ustilago Avenae* (Pers.) Jens.) and covered (*Ustilago levis* (K. & S.) Magn.) smuts has been determined. The Missouri races of the smuts were used for inoculation, since the existence of specialized races (30, 32) of loose and covered smuts makes it highly important to use definite races whose capacity for infecting parental varieties is fully known.

DESCENDANTS OF CROSSES BETWEEN HULL-LESS AND BLACK MENDAG

DESCRIPTION OF THE PARENTS

The progenies of four different hybrids (Nos. 10, 11, 12 and 13) between Hull-less and Black Mesdag have been studied. The crosses were made in 1925 in the greenhouse and in every case Hull-less was used as the female parent and Black Mesdag as the male. The Hull-less or naked oats are regarded as belonging to a distinct species, *Avena nuda* L., and are distinguished from the other species of *Avena* by several characteristics, the most important of which are: (1) The lemma and palea do not clasp the kernel, the latter remaining loose or free within the chaff, and readily separating in threshing; (2) the empty glumes and lemmas are very similar in texture, being thin and membranous; (3) each spikelet of the panicle bears several flowers, varying from four to nine; and (4) the rachillas of the spikelets are much elongated so that the uppermost grains are borne well above the empty glumes. The female plant used belonged to the variety *inermis*, which is almost completely lacking in awns. The plant is erect in growth, tillering to a moderate extent; the leaves are rather narrow and light green in color; the panicles are equilateral and compact with a fairly large number of

branches; the spikelets of the panicle are many-flowered, usually four to six.

Black Mesdag is a typical hulled oat belonging to *Avena sativa* L. The plant is erect in growth, tillering only to a slight degree. The leaves are relatively broad, dark green in color, with smooth margins. The panicles are equilateral, wide-spreading and very lax, drooping from the middle outward. The spikelets bear usually two grains, rarely three. The lemmas and paleae are brownish black and glabrous; well developed awns are usually present on the lower grain of each spikelet.

Both of these varieties have been repeatedly tested for their behavior to the Missouri races of loose and covered smuts (29, 35). Hull-less has consistently shown a high degree of susceptibility and under favorable conditions one hundred per cent infection has usually been obtained. On the other hand, Black Mesdag has proved to be one of the most resistant varieties of oats experimented with. Under all types of conditions it has uniformly remained practically free from infection by either smut.

THE F₁ GENERATION

The four F₁ plants were grown in the greenhouse in 1926. They were very similar in appearance, with stems erect in growth and tillering to a greater extent than either parent, giving rise to several stalks on each plant. The leaves were broad and dark green in color, thus resembling the Black Mesdag parent. The panicles were rather long, spreading and drooping somewhat from the middle outward. In general shape they resembled the Black Mesdag parent with, however, a larger number of branches and spikelets. On two of the plants all the spikelets were many-flowered, the number of grains produced being from two to five. The empty glumes and lemmas were entirely similar to those of the Hull-less, the lemmas yellow in color and membranous in texture; the paleae, however, were dark. The grains were held loosely in the glumes, readily falling out in threshing. Very weak or feeble awns were present on the basal flowers of a few spikelets, being slightly more numerous than on the Hull-less parent. The other two F₁ plants resembled very closely those just described. There were present, however, a few spikelets in which the lemma had developed into a hard ridge and in the upper spikelets the kernel was held more or less securely within the glumes. On one of the plants there were only two or three of these spikelets, while on the other they were somewhat more numerous. In general all four plants resembled a somewhat more robust type of the Hull-less parent; the broader leaves, the longer, more lax and drooping panicles,

together with the dark color of the paleae, were the most marked points of difference.

EXPERIMENTAL RESULTS WITH F_2 GENERATION

The fact that the infection of oats by both loose and covered smut takes place in the young seedling and that, if it does occur, it usually results in the complete destruction of the grain, necessitates a modification of the procedure of analyzing the inheritance of smut resistance. Accordingly, the seeds which developed into the F_1 plants were not inoculated and thus their resistance or susceptibility was not determined. The seeds of these plants, however, were divided into three lots. One lot was left without any inoculation, a second was inoculated with the spores of loose smut and the third was inoculated with the spores of covered smut, and thus three sets of F_2 plants were grown.

Since various environal conditions, as soil temperature, soil moisture and soil reaction, influence the infection of susceptible varieties of oats, special attention was given to securing the most favorable conditions (34). The inoculated seeds were planted in sand with a moisture content of about 20 per cent. They were then placed in the constant-temperature tank and held at 20° C. After the seedlings had appeared above the level of the sand they were transplanted, each one into a separate six-inch pot, where they were allowed to grow to maturity. Very few seeds failed to germinate and practically all of the seedlings developed into vigorous plants.

The results obtained with these four progenies are presented in Table 1.

TABLE 1

Results with Inoculated F_2 Plants of Crosses between Hull-less (Seed No. 30) and Black Mesdag (Seed No. 70)

	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Hybrid No. 10	115	22	19.1	49	12	24.4
Hybrid No. 11	116	30	25.8	49	9	18.3
Hybrid No. 12	115	27	23.4	49	6	12.2
Hybrid No. 13	119	28	23.5	49	13	26.5
	465	107	23.0	196	40	20.4
Hull-less	28	28	100.0	22	22	100.0
Black Mesdag	28	0	0	28	0	0

Results with Ustilago Avenae.—A total of 465 plants of the four crosses, inoculated with *Ustilago Avenae*, was grown and 107, or 23 per cent, of these were infected. The four families gave quite similar results; the lowest percentage of infection was 19.1 per cent in hybrid No. 10, and the highest was 25.8 per cent in hybrid No. 11. Along with these F_2 plants there were grown inoculated plants of both parents. The susceptible Hull-less plants were all infected while those of the resistant Black Mesdag showed no evidence of smut.

Results with Ustilago levis.—In the series with *Ustilago levis* 196 plants were inoculated and 40 plants, or 20.4 per cent, were infected. There was a rather wide range of variation between the different families, since hybrid No. 12 gave only 12.2 per cent infection while hybrid No. 13 gave 26.5 per cent. The inoculated plants of the susceptible parent grown in conjunction with the hybrids were all infected, while none of the resistant Black Mesdag showed any smut. The results correspond fairly well with those obtained with loose smut and indicate a similar mode of inheritance of the smut-resistant quality.

The data with both smuts indicate quite clearly that resistance is a dominant character and that susceptibility is recessive. Further, they suggest that there is a single factor difference between resistance and susceptibility, thus giving a simple mono-hybrid ratio of three resistant to one susceptible F_2 plants.

BEHAVIOR OF THE F_3 GENERATION

In view of the close harmony in the behavior of the F_2 plants to both smuts, the reaction of the F_3 progenies becomes of the greatest importance. On account of the methods used in connection with the F_2 generation, the progenies of three different groups of F_2 plants were available for study: (1) Plants whose F_2 parent was not inoculated with either smut; (2) F_2 plants resistant to *Ustilago Avenae*; and (3) F_2 plants resistant to *U. levis*.

In planning the experiments with the F_3 generation, seeds from the F_2 plants belonging to each of these three groups were taken and divided into two lots of twenty seeds each, one lot being inoculated with spores of loose smut and the other with spores of covered smut. By this method some individuals of the progenies of each F_2 plant were subjected to the possibility of infection with each smut. The methods employed were similar to those used in connection with the F_2 plants, the inoculated seeds being planted in sand with 20 per cent moisture and germinated at a constant temperature of 20° C. When the seedlings had attained

TABLE 2
Summary of Results with F_2 families of crosses between Hull-less and Black Meslay

	No. of families grown	Similar reaction to <i>Ustilago Avenae</i> and <i>U. levis</i>			Dissimilar reaction to <i>Ustilago Avenae</i> and <i>U. levis</i>		
		Resistant	Segregating	Susceptible	Resistant to <i>Avenae</i> Segregating to <i>levis</i>	Resistant to <i>levis</i> Segregating to <i>Avenae</i>	Susceptible to <i>Avenae</i> Segregating to <i>levis</i>
F ₂ families descended from uninoculated F ₂ plants							
Hybrid No. 10.....	49	18	18	9	1	3	0
" " 11.....	46	14	21	7	0	0	4
" " 12.....	49	14	19	7	2	5	2
" " 13.....	50	10	24	14	2	0	0
	194	56	82	37	5	8	6
F ₂ families descended from F ₂ plants inoculated with <i>Ustilago Avenae</i>							
Hybrid No. 10.....	74	30	39	0	1	2	2
" " 11.....	70	24	38	0	3	5	0
" " 12.....	70	21	45	0	1	2	1
" " 13.....	72	23	47	0	1	0	1
	286	98	169	0	6	9	4
F ₂ families descended from F ₂ plants inoculated with <i>Ustilago levis</i>							
Hybrid No. 10.....	25	6	16	0	1	2	0
" " 11.....	25	7	15	1	1	1	0
" " 12.....	23	5	14	1	0	3	0
" " 13.....	25	7	17	0	0	0	1
	98	25	62	2	2	6	1

a suitable size, they were transplanted either to the greenhouse bench or to the field.

The results with the F_3 generation are summarized in Table 2 and presented in detail in the supplementary Tables A to L. In all these tables the families are classified on the basis of their behavior with reference to both smuts. The progenies which gave a similar reaction—either resistant, segregating or susceptible to both loose and covered smut—are grouped together and the remaining progenies which behaved differently with reference to the two smuts are likewise combined. Supplementary Table M is a summary of Tables A to L, showing the total number of individuals grown in the F_3 progenies which behaved in a similar manner.

Results with F_3 Families Descended from Uninoculated F_2 Plants.—As noted above, the data obtained with the inoculated F_2 plants suggested a simple Mendelian ratio in which resistance to smut was dominant and susceptibility recessive. If this interpretation of the F_2 data is correct, then we may expect three classes of progenies descended from the uninoculated F_2 plants: (1) All the individuals resistant; (2) all the individuals susceptible, and (3) a class in which the progeny shows segregation for smut resistance. Further, these three groups of families should appear in a ratio approximating one susceptible, two segregating and one resistant.

In classifying the families, those in which all the individuals remained free from infection were designated as "resistant;" those in which the infection was greater than 50 per cent were grouped as "susceptible;" those in which less than 50 per cent of the individuals were infected were set down as "segregating." Usually in the susceptible families more than 80 per cent, and frequently 100 per cent, were infected. When the percentage of infection was only slightly above 50 per cent, there might be uncertainty whether the family should be classified as susceptible or as segregating. This arbitrary division line was applied, however, although further experiments are planned to determine whether the families on the border have been classified properly.

As may be seen from Table 2, 49 families of hybrid No. 10 were grown, and 45 of these showed a similar behavior to both smuts. Of this total, 18 families were classified as resistant, since none of the individuals showed any infection, 18 families were classified as segregating, since the percentage of infection in each ranged from 6 to 45 per cent, and 9 families proved to be susceptible, 64 to 100 per cent of the individuals being infected. Of the remaining 4 families one proved to be

resistant to *Ustilago Avenae*, while segregating to *U. levis*, and 3 were resistant to *U. levis* and segregating to *U. Avenae*.

There were grown 46 families of hybrid No. 11 and 42 of these behaved in a similar manner to both smuts, 14 being classified as resistant, 21 as segregating and 7 as susceptible. The remaining 4 families gave high percentages of infection with *U. Avenae* but low ones with *U. levis*.

Hybrid No. 12 was represented by 49 families, of which 40 showed a similar behavior to both smuts, 14 being resistant, 19 segregating and 7 susceptible. Two additional families were resistant to *U. Avenae* but segregating to *U. levis*; 5 families were resistant to *U. levis* but segregating to *U. Avenae* and 2 families gave high percentages of infection with *U. Avenae* and low ones with *U. levis*.

There were grown 50 families of hybrid No. 13, 48 showing a similar behavior to both smuts. These families were classified as 10 resistant, 24 segregating and 14 susceptible; the remaining 2 families proved to be resistant to *U. Avenae* while segregating to *U. levis*.

A total of 194 families of the four hybrids was grown and all but 19 gave a similar reaction to loose and covered smut; 56 of these were entirely resistant, 82 segregating and 37 susceptible.

The uninoculated F_2 plants of each of the four hybrids gave progenies belonging to all of the three expected classes—pure resistant, segregating and pure susceptible. The number of resistant families, however, was too large to fit a 1 : 2 : 1 ratio. The 56 resistant families contained 928 plants which had been inoculated with *Ustilago Avenae* and 940 inoculated with *U. levis* without a single plant being infected. The 37 susceptible families contained 655 plants inoculated with *U. Avenae*, 611, or 93.2 per cent, being infected; 635 plants of these same families were inoculated with *U. levis* and 519, or 81.7 per cent, were infected. The 82 segregating families contained 1397 individuals inoculated with *U. Avenae* and 323, or 23.1 per cent, were infected. There were 1380 plants inoculated with *U. levis*, of which 279, or 20.2 per cent, were infected.

*Results with F_2 Families Descended from F_2 Plants Resistant to *Ustilago Avenae*.*—Of this group 286 families were grown and, as they were all descended from F_2 plants which had escaped infection with loose smut, we should expect the appearance of two classes: One in which all the individuals are resistant and one in which segregation for smut resistance occurs. Further, the number of families should occur in the proportion of one resistant to two segregating.

As noted in Table 2 a total of 267 of these families gave similar

results with both smuts, 98 proving to be pure resistant and 169 segregating. Of the remaining 19 families 6 were resistant to *Ustilago Avenae* and segregating to *U. levis*, 9 resistant to *U. levis* and segregating to *U. Avenae*, 4 susceptible to *U. Avenae* and segregating to *U. levis*. These last 4 families, however, gave infections only slightly above 50 per cent. The actual results with each smut were as follows: Hybrid No. 10 F₃-107 gave 60 per cent infection with *U. Avenae* and 36.3 per cent with *U. levis*; hybrid No. 10 F₃-180 gave 52.9 per cent infection with *U. Avenae* and 20 per cent infection with *U. levis*; hybrid No. 12 F₃-168 gave 52.6 per cent with *U. Avenae* and 35.2 per cent with *U. levis*; and hybrid No. 13 F₃-145 gave 57.1 per cent infection with *U. Avenae* and 23.5 per cent with *U. levis*. It is quite possible that actually these 4 families should be classified as segregating.

The 98 resistant families contained 1529 individuals inoculated with *U. Avenae* and 1668 inoculated with *U. levis*. There were 2665 plants in the 169 segregating families inoculated with *U. Avenae*, of which 659, or 24.7 per cent, were infected. These families contained 2882 plants inoculated with *U. levis* and 604, or 20.9 per cent, were infected.

Results with F₃ Families Descended from F₂ Plants Resistant to Ustilago levis.—The descendants of 98 F₂ plants of this group were grown and 89 progenies gave similar results with both loose and covered smut; 25 families being resistant, 62 segregating and 2 being susceptible. These two susceptible families gave the following results: Hybrid No. 11 F₃-62 gave 100 per cent infection with *Ustilago Avenae* and 61.1 per cent infection with *U. levis* and hybrid No. 12 F₃-76 gave 100 per cent infection with *U. Avenae* and 82.3 per cent infection with *U. levis*. A possible explanation of the appearance of these 2 susceptible families in this group is that the F₂ parent, although inoculated, escaped infection, for susceptible individuals sometimes do not show the infection.

The remaining 9 families gave a different behavior with the two smuts, 2 proving to be resistant to *U. Avenae* and segregating to *U. levis*, 6 resistant to *U. levis* and segregating to *U. Avenae*, and one, hybrid No. 13 F₃-66, susceptible to *U. Avenae* (57.8 per cent infected plants) and segregating to *U. levis* (22.2 per cent infected plants).

The 25 resistant F₃ cultures contained 434 plants in the series with loose smut and 430 in the series with covered smut. The 62 segregating cultures in the loose smut series consisted of 1132 plants of which 254, or 22.4 per cent, were infected, and in the covered smut series there were 1108 individuals, of which 229, or 20.6 per cent, were infected.

One of the most interesting features of the results is the fact that the

different F_2 plants and their progenies behaved so nearly alike to both loose and covered smut. A total of 518 F_1 families were grown and 531 were readily classified as either resistant, segregating or susceptible to both smuts. Only 47 families gave a dissimilar reaction. In general, then, an F_1 family resistant to one smut is practically certain to be resistant to the other, and a family susceptible to one is susceptible to the other. The exceptions to this broad statement may in part be explained on the basis of accidental occurrences in the course of the experiments. Some of the discrepancies observed may be due to the fact that it is difficult to be certain of the infection of all susceptible individuals. In our methods we have endeavored to eliminate the unfavorable conditions for infection as completely as possible. In handling such large numbers of plants, however, it is not easy to be certain that all favorable conditions have been fully supplied. On the other hand, it is quite possible that some of the progenies actually do differ in their behavior toward the smuts. Special experiments are now being carried out with these exceptional families in order to determine just what the situation actually is.

It will be observed from the general summaries given in connection with each group of F_1 cultures that a higher percentage of plants was infected in the loose smut series than in the covered smut series. However, I do not believe that there is any special significance to be attached to this difference. Both parents were grown along with the F_1 generation; 65 plants of Hull-less were inoculated with *Ustilago Avenae* and 59, or 90.7 per cent, were infected. In the *U. levis* series 80 plants of Hull-less were inoculated and 47, or 58.7 per cent, were infected. In these cultures, then, some individuals of the susceptible parent escaped. The resistant parent gave no infection with either smut, 51 plants being inoculated with *U. Avenae* and 88 with *U. levis*.

Just why there should be such a parallelism in the behavior of the two smuts is an interesting problem. These organisms are distinct species, being differentiated by the following features: The spores of *Ustilago Avenae* are roughened while those of *U. levis* are smooth. A more complete destruction of the floral parts of the oat is brought about by the loose smut and the spores are more widely distributed before harvest as compared with the covered. Further, the species do show differences in their ability to attack oat varieties. While the great majority of oats are readily attacked by both smuts and a few varieties are resistant to both, there are some varieties which are resistant to one but susceptible to the other.

THE F₂ GENERATION OF CROSSES BETWEEN SILVERMINE AND BLACK MESDAG

The progeny of two crosses between Silvermine (Seed No. 164) and Black Mesdag (Seed No. 70) were tested with both smuts. Silvermine is a hulled oat with medium long panicles which are broad but somewhat compact, stiff and erect. The spikelets are two to three-grained; the grains are white to yellowish white; the awns are wanting or relatively few in the panicle and rarely twisted. It is a valuable variety, medium late in maturing, but it has proved to be quite susceptible to both smuts under field conditions. It has not been extensively grown in specially controlled experiments, but in these it has proved to be completely susceptible.

The results with these two hybrids are given in Table 3.

TABLE 3

Results with Inoculated F₂ Plants of Crosses between Silvermine (Seed No. 164) and Black Mesdag (Seed No. 70)

	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Hybrid No. 17	47	11	23.4	46	5	10.8
Hybrid No. 18	48	6	12.5	43	10	23.8
	95	17	17.8	89	15	16.8
Black Mesdag	15	0	0	15	0	0
Silvermine	15	15	100.0	9	9	100.0

There were 95 F₂ plants inoculated with *Ustilago Avenae* and 17, or 17.8 per cent, were infected; 89 F₂ plants were inoculated with *U. levis* and 15, or 16.8 per cent, were infected. The inoculated plants of Black Mesdag in the same experiment gave no infection, while Silvermine gave 100 per cent infection with each smut.

Again we observe that resistance to both smuts is dominant. Hybrid No. 17 gave a greater percentage of infection with *U. Avenae*, while hybrid No. 18 gave a higher infection with *U. levis*.

CROSSES BETWEEN SUSCEPTIBLE OAT VARIETIES

The F_2 descendants of a cross (hybrid No. 14) between Canadian (Seed No. 119) and Victor (Seed No. 126) were tested with the Missouri races of both smuts. The main feature of interest in these experiments is based on the fact that both these varieties are extremely susceptible to loose and covered smut.

Victor is a hulled oat, erect in growth and medium late in maturing. It has long, broad, coarse, wide-spreading panicles. The spikelets are usually two-grained; the grains are black to brownish black, very large and coarse. Strong awns are usually present, twisted at the base and often geniculate. Canadian is also a hulled oat, erect in growth and medium early in maturing. It has long lax panicles which droop at the apex. The spikelets are predominantly two-grained; the grains are white to pale yellow, short and plump. Awns are commonly present, but seldom twisted and rarely geniculate. Both Canadian and Victor have proved to be extremely susceptible to smuts. In ordinary field plantings it is quite common to obtain more than 50 per cent infection and, when these varieties are grown under carefully controlled conditions, usually all the plants become infected.

The cross between Canadian and Victor was made in 1924 and the F_1 plant was grown in 1925. In 1926 the experiments with the F_2 plants were carried out, the data obtained being presented in Table 4.

TABLE 4

Results with Inoculated F_2 Plants of Crosses between Susceptible Oat Varieties.—Canadian (Seed No. 119) × Victor (Seed No. 126) and Silvermine (Seed No. 164) × Hull-less (Seed No. 30)

	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Hybrid No. 14. Canadian × Victor	91	91	100.0	42	42	100.0
Hybrid No. 15. Silvermine × Hull-less	53	53	100.0
Canadian	28	28	100.0	19	19	100.0
Victor	19	19	100.0	22	22	100.0
Silvermine	26	26	100.0
Hull-less	29	29	100.0

There were 91 F_2 plants of the hybrid grown in the series with *Ustilago Avenae* and 42 F_2 plants in the series with *U. levis*. All of these inoculated plants became infected and in the parallel experiments the inoculated plants of the parents also gave 100 per cent infection.

The F_2 plants of a cross between Silvermine (Seed No. 164) and Hull-less (Seed No. 30) were also studied, 53 F_2 plants being inoculated with *Ustilago Avenae*, and all became infected. The control experiments with the parents also gave complete infection with this smut.

It is evident that all the individuals of these crosses between two susceptible parents are readily attacked by the smuts.

CROSSES BETWEEN A VARIETY SUSCEPTIBLE TO BOTH SMUTS AND A VARIETY SUSCEPTIBLE TO USTILAGO AVENAE BUT RESISTANT TO U. LEVIS

A cross (hybrid No. 16) was made between Early Gothland (Seed No. 152) and Victor (Seed No. 126). The former has proved to be very susceptible to loose smut while it has consistently shown a high degree of resistance to covered smut, while Victor is highly susceptible to both smuts. Early Gothland is a hulled oat and is a late maturing variety. It has long spreading panicles, often drooping at the apex, although the branches are usually ascending. The spikelets are usually two- to three-grained; the grains are white to yellowish white and elongate. The awns are numerous in the panicle, but usually are not twisted. This variety has been tested in numerous experiments and has shown a marked susceptibility to *Ustilago Avenae*, under favorable conditions all the plants being infected. It has shown an equally strong resistance to *U. levis*. It is accordingly a matter of great interest to determine how the descendants of Early Gothland and Victor react to each of the two smuts. The data for the F_2 generation of this cross are shown in Table 5.

In a series with *Ustilago Avenae*, 52 plants of the F_2 generation were inoculated and all of them became infected. The results were entirely similar to those obtained with crosses between Canadian and Victor, and Silvermine and Hull-less.

On the other hand, 44 F_2 plants of this cross were inoculated with *U. levis*, to which Early Gothland is resistant, and only 8 plants, or 18.1 per cent, were infected. In this case, where one of the parental varieties is susceptible and the other resistant to the smut used, we get a segregation into resistant and susceptible individuals with resistance as dominant and a ratio approaching more or less the usual three to one.

TABLE 5

Results with Inoculated F_2 Plants of Crosses between Victor (Seed No. 126) or Hull-less (Seed No. 30), Varieties Susceptible to both *Ustilago Avenae* and *U. teris*, and Early Gothland (Seed No. 152), Susceptible to *U. Avenae* but Resistant to *U. teris*

	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago teris</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Hybrid No. 19. Early Gothland × Hull-less	24	22	91.6	49	18	36.7
Hybrid No. 20. Early Gothland. × Hull-less	22	21	95.4	45	19	42.2
	46	43	93.4	94	37	39.3
Hybrid No. 16. Early Gothland × Victor	52	52	100.0	44	8	18.1
Early Gothland	30	30	100.0	30	0	0
Victor	25	25	100.0	22	22	100.0
Hull-less	14	13	92.8	15	14	93.3

Two crosses (hybrids No. 19 and No. 20) between Early Gothland and Hull-less were also studied. As repeatedly noted, the latter variety is extremely susceptible to both loose and covered smut. There were 24 F_2 plants of hybrid No. 19 and 22 plants of hybrid No. 20 inoculated with *U. Avenae*. Practically all of these were infected, only 3 plants out of a total of 46 escaping. On the other hand, 49 plants of hybrid No. 19 and 45 plants of hybrid No. 20 were inoculated with *U. teris*. As seen in Table 5, 18 plants (36.7 per cent) of the former and 19 plants (42.2 per cent) of the latter were infected. Again we obtain a segregation to this smut with resistance as dominant, although the number of susceptible individuals is rather too large to fit very closely a three to one ratio.

CROSSES BETWEEN HULL-LESS (SEED NO. 30), SUSCEPTIBLE TO BOTH SMUTS, AND MONARCH (SEED NO. 161), SUSCEPTIBLE TO *USTILAGO LEVIS* BUT RESISTANT TO *U. AVENAE*

Hybrids between Monarch and Hull-less are the complements of those just described. Monarch has usually shown a very high degree of resistance to *Ustilago Avenae* and extreme susceptibility to *U. levis*. This applies especially to the Missouri races of both smuts. So far as known, the variety is very susceptible to practically all races of *U. levis*. It is, however, susceptible to some races of *U. Avenae* but resistant to others.

Monarch is a hulled oat, medium early in maturing. It has wide-spreading lax panicles, the branches drooping from the middle outward. The spikelets are usually two-grained; the grains are brownish black and elongate. Awns are usually numerous in the panicle, but are rarely twisted at the base.

Four crosses involving Monarch and Hull-less were made. In hybrid No. 24 Monarch was the female parent and Hull-less the male, and in hybrids Nos. 25, 26 and 27 Hull-less was the female parent and Monarch the male. The data are recorded in Table 6.

TABLE 6

Results with Inoculated F_2 Plants of Crosses between Hull-less (Seed No. 30), Susceptible to both *Ustilago Avenae* and *U. levis*, and Monarch (Seed No. 161), Susceptible to *U. levis* but Resistant to *U. Avenae*

	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Hybrid No. 24. Monarch × Hull-less	49	12	24.4	25	22	88.0
Hybrid No. 25. Hull-less . . . × Monarch	50	11	22.0	27	27	100.0
Hybrid No. 26. Hull-less . . . × Monarch	48	7	14.5	23	22	95.6
Hybrid No. 27. Hull-less . . . × Monarch	49	11	22.4	25	24	96.0
	196	41	20.9	100	95	95.0
Hull-less	14	13	92.8	15	14	93.3
Monarch	15	0	0	15	15	100.0

In the series with *Ustilago levis*, to which both parents are susceptible, 100 F_2 plants of the four crosses were inoculated, and 95 became infected. A correspondingly high infection of both parents was obtained in the parallel series of experiments, 14 plants out of 15 of Hull-less and all 15 plants of Monarch being infected.

There were 196 F_2 plants of the four families inoculated with *U. Arenae* and 41, or 20.9 per cent, were infected. There was considerable variation among the different families, the percentage of infection in hybrid No. 26 being as low as 14.5 per cent and in hybrid No. 24 as high as 24.4 per cent. Each family, however, showed segregation for resistance to loose smut more or less closely approaching the three-to-one ratio, with resistance as dominant. The resistant parent, Monarch, remained free from infection, while all the plants of the susceptible Hull-less except one were infected.

DISCUSSION

It is beyond the scope of the present paper to discuss in detail the extensive literature on the inheritance of disease resistance in plants. Practically all of the investigations date from the interesting results of Professor R. H. Biffen, first published in 1905, with reference to the behavior of certain wheat hybrids to yellow rust, *Puccinia glumarum* (Schm.) Erikss. and Henn. Since that time extensive researches have been carried on in this field. For the most part they have dealt with the rusts and smuts of cereals, since these host plants, as well as their parasites, lend themselves very readily to such studies. In addition to their being favorable material, the economic importance of these crops and the value of resistant varieties which combine desirable agronomic characters have stimulated the investigations.

With reference to the rusts of cereals it is interesting to note that Biffen (4, 5, 6) in his crosses found that susceptibility was dominant and resistance recessive to the yellow rust, and segregation in the F_2 appeared to take place on the basis of a single factor difference. Armstrong (2), working with similar material, has confirmed Biffen's conclusions. Nilsson-Ehle (26), however, working with other varieties of wheat, has found a more complicated condition in the inheritance of resistance to yellow rust.

Extensive investigations have been carried on with reference to resistance to stem rust (*Puccinia graminis* Pers.) in hybrids of wheat. Hayes, Parker and Krutzweil (20), Puttick (28), Waldron (39), Melchers and Parker (25), Aamodt (1), Harrington and Aamodt (18),

Hayes and Aamodt (19), Clark (8), Harrington (17), Hayes, Stakman and Aamodt (21), have studied a large number of different crosses involving varieties of various degrees of susceptibility and resistance to known races of rust. The results obtained have varied greatly. In some cases susceptibility has been dominant and in others resistance. In some of the hybrids a simple mono-hybrid segregation occurred in the F_2 while in other hybrids the mode of inheritance was much more complex.

Garber (15) found that resistance to stem rust in oat hybrids was dominant and that segregation occurred among the F_2 plants in a three to one ratio. Griffiee (16) confirmed these results in a study of the same material in later generations.

Mains, Leighty and Johnston (23) have studied the inheritance of resistance to leaf rust (*Puccinia triticina* Erikss.) in certain wheat crosses and, in general, they found that resistance was dominant and segregation occurred on the mono-hybrid basis. Tochinal and Kihara (37) have studied the correlations between morphological characters and chromosome number and resistance to the same rust. In segregates of durum and common wheat they observed that those resembling durum in morphological characters and chromosome number were resistant, while those resembling the common wheat in their morphological character and chromosome number were susceptible. Similar results were obtained with crosses involving other varieties and species of wheat.

Parker (27) found that susceptibility to crown rust (*Puccinia coronata* Corda) was dominant in crosses between Sixty-day and Burt oats. He did not analyze his results in detail, but concluded that resistance and susceptibility did not depend on a single factor. Davies and Jones (9, 10), on the other hand, have studied this problem in connection with Potato and Red Rustproof oats; they found that resistance was dominant and a typical mono-hybrid segregation occurred in the F_2 generation.

Biffen (5) has recorded his data on a hybrid between two barleys, one of which (*Hordeum spontaneum*) was resistant to powdery mildew (*Erysiphe graminis* DC.) and the other variety, a six-rowed barley, was susceptible. The F_1 plants were noticeably susceptible and in the F_2 generation a segregation occurred giving approximately three susceptible to one resistant.

Hayes, Stakman, Griffiee and Christensen (22) noted the susceptibility of F_2 lines of Manchuria and Lion barley hybrids with reference to *Helminthosporium sativum*. Some of the families were as resistant

as Manchuria and others as susceptible as Lion, but these depended on more than a single genetic factor. They also found a greater proportion of resistant families with white seeds and rough awns, similar to the resistant Manchuria parent, and a larger proportion of susceptible had the combination of black seeds and rough awns. It was possible, however, to secure combinations of resistance and susceptibility with the various morphological characters.

McRostie (24) found that resistance to Anthracnose in certain bean crosses was dominant. The F_2 generation of a cross between a resistant and susceptible variety segregated on the basis of a three to one ratio when inoculated with a single strain of the fungus. When, however, two strains were used, a ratio of 9 resistant to 7 susceptible was obtained.

Gaines (11, 12, 13) and Gaines and Singleton (14) have studied the inheritance of resistance in several wheat hybrids to bunt (*Tilletia tritici* (Bjerk.) Wint.) and have obtained very complicated results. The varieties crossed appeared to vary greatly in their degree of resistance to this smut and all sorts of degrees of resistance were found in the progenies.

Briggs (7) studied the inheritance of bunt resistance in crosses between Martin and Hussar and certain susceptible varieties. He found that, when Martin was crossed with Hard Federation, Baart and White Federation, resistance was completely dominant and the F_2 segregated on the basis of a single factor for resistance. On the other hand, his results with Hussar and Hard Federation and Hussar and Baart indicated the occurrence of two dominant factors for resistance, one of which seemed to be identical with the factor found in Martin.

In addition to my earlier paper (31) a few results on the study of inheritance of oat smut have been recorded. Wakabayashi (38) observed no covered smut (*Ustilago loris*) in the F_1 and F_2 plants of a cross between Red Rustproof and Black Tartarian oats. In the F_1 generation a few families contained a small number of infected individuals. Gaines (13) has recorded some results of crosses between resistant Red Rustproof and the more or less susceptible varieties as Black Tartarian, Abundance and Large Hull-less. In all three crosses resistance is dominant and relatively few susceptible families in the F_1 were isolated. Barney (3) studied various oat crosses and interpreted his results obtained with Fulghum and Black Mesdag on the basis of a three-factor difference. On the other hand, his results with Burt and Swedish Select suggested a two-factor difference and those with Turkish Rustproof and Golden Rain a one-factor difference. Reed

and Stanton (36) studied the F_2 progeny of crosses between Fulghum and Swedish Select. Some of these showed a degree of susceptibility corresponding to that of the susceptible Swedish Select parent. Other cultures showed a somewhat greater susceptibility and a few possessed a resistance corresponding to that of Fulghum.

From this brief review it may be noted that resistance is sometimes dominant in inheritance and in other cases is recessive. Several of the investigators have found that a segregation occurs in the F_2 on the basis of a single factor difference, or in a typical mono-hybrid ratio. Others have found a more complicated situation and, in view of the great differences in some of the crosses made and the differences in the behavior of the parents toward the races of parasites, we might expect hereditary relations to be more complicated in some crosses than in others.

An exact knowledge of the mode of inheritance of disease resistance is a forward step in obtaining new valuable varieties of crop plants. A formidable difficulty in developing resistant varieties is that of obtaining resistance without loss of any other desirable features. Many things enter into the composition of a successful variety of oats: adaptation to local environment; stiffness of straw and ability to withstand lodging; length of time required for maturity; non-shattering of the grain in harvesting operations; quality of grain; cropping capacity or yield. Further, it requires a long time to develop a new strain. Starting with the making of the cross, eight to ten years must elapse before the capacity of the new selection is sufficiently tested and an ample supply of seed is available for wide distribution. In the meantime, many promising selections have fallen by the wayside because of their lacking some essential feature which would enable them to compete successfully with present-day varieties.

One important fact, however, stands out, and that is the possibility of the recombination of desirable agronomic characters with disease resistance. The resistant parent frequently possesses some undesirable qualities which render it unadapted to present conditions. Occasionally we find varieties in cultivation which do possess valuable qualities—Fulghum and Red Rustproof oats are very resistant to many races of oat smut; Hussar and Martin wheat have manifested a similar resistance to races of hant; Feterita and the Milos are very resistant to certain smuts of sorghum. All these varieties possess great merits as crop plants, as they are well adapted to certain localities. Not their least value, however, is the possibility of using them for the improvement of other local varieties by bringing their quality of disease resistance into combination with other characters.

Generally, however, the resistant types are handicapped by lacking one or more essential qualities. Frequently they are brought in from other agricultural regions and, while they may be poor-looking sorts as compared with the local varieties, yet they may add the disease-resistant quality to the hybrids.

Several investigators have found some linkage in the hybrids between disease resistance and certain undesirable morphological features. However, this linkage does not appear in any case to be complete and thus the possibility of securing valuable resistant strains may be realized. So far as my own studies with oats are concerned, there appears to be no obvious linkage between resistance and other characters. As yet, however, I have considered this question beyond the F_2 generation only in crosses involving Hull-less and Black Mesdag. So far as the other hybrids are concerned, the F_2 plants show the expected combinations of characters with disease resistance. In the descendants of the crosses of Hull-less and Black Mesdag it has been possible to secure a great variety of types. True breeding selections of Hull-less oats which possess the marked resistance of the original Black Mesdag have been secured. Other types closely resembling the resistant Black Mesdag, but possessing a high degree of susceptibility, have also been obtained. And, most important of all, diverse combinations of the parental characters have been attained in numerous selections.

SUMMARY

1. The F_2 and F_3 generations of crosses between Hull-less and Black Mesdag oats have been studied with reference to their behavior to loose and covered smut. The former is susceptible to both smuts, while Black Mesdag is resistant. The results may be summarized as follows:
 - A. There were 465 F_2 plants inoculated with loose smut and 107 (23 per cent) were infected.
 - B. There were 196 F_2 plants inoculated with covered smut, and 40 (20.4 per cent) were infected.
 - C. A total of 590 F_3 families inoculated with each of the smuts was grown. Of these 541 gave a similar reaction to the two smuts, the remaining 49 manifesting a dissimilar behavior.
 - D. The F_2 data strongly suggest a single factor difference for resistance in these two varieties, and the data on the F_3 generation are in relatively close correspondence with this interpretation.

2. The F_2 generation of a cross between the susceptible Silvermine and resistant Black Mesdag gave similar results: 95 F_2 plants inoculated with loose smut gave 17.8 per cent infection and 89 F_2 plants inoculated with covered smut gave 16.8 per cent.
3. Crosses between certain susceptible varieties (Canadian \times Victor and Silvermine \times Hull-less) were made and the behavior of the F_2 descendants determined. In every case they were as susceptible as the original parental varieties.
4. Crosses between the varieties Hull-less and Victor, susceptible to both smuts, and the variety Early Gothland, susceptible to loose smut, were studied. The F_2 plants of Early Gothland \times Victor gave 100 per cent infection with loose smut, 52 plants being inoculated, while 8 plants out of 44 (18.1 per cent) were infected with covered smut. With the hybrid Early Gothland \times Hull-less 93.4 per cent of the F_2 plants inoculated with loose smut were infected. Of the 94 F_2 plants inoculated with covered smut 37 (39.3 per cent) were infected.
5. Similarly, crosses between the variety Hull-less, susceptible to both smuts, and the variety Monarch, susceptible to covered smut but resistant to loose smut, were made. There were 196 F_2 plants inoculated with loose smut and 41 (20.9 per cent) were infected. On the other hand, 95 of the 100 F_2 plants inoculated with covered smut were infected.
6. In all the crosses involving varieties differing in their behavior to smut, resistance was dominant and susceptibility recessive, and segregation in the F_2 appeared to occur on the basis of a single factor difference.
7. The recombination of smut resistance with various desirable characters may be successfully accomplished.

SUPPLEMENTARY TABLES A-M

RESULTS WITH F_3 FAMILIES OF HYBRIDS BETWEEN HULL-LESS
AND BLACK MESDAG

TABLE A

Results with F_3 Families of Hybrid No. 10 Descended from
Uninoculated F_1 Plants

F_3 Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F_3 families						
1	16	0	0	17	0	0
3	17	0	0	16	0	0
5	20	0	0	17	0	0
8	20	0	0	18	0	0
14	19	0	0	18	0	0
18	18	0	0	17	0	0
20	18	0	0	19	0	0
21	19	0	0	17	0	0
23	10	0	0	19	0	0
25	19	0	0	20	0	0
27	18	0	0	16	0	0
31	16	0	0	17	0	0
32	16	0	0	16	0	0
34	16	0	0	17	0	0
39	19	0	0	18	0	0
43	18	0	0	17	0	0
47	11	0	0	12	0	0
50	16	0	0	18	0	0
Segregating F_3 families						
4	19	7	36.7	19	2	10.5
6	16	3	18.7	17	2	11.7
7	19	5	26.3	10	1	10.0
9	19	3	15.7	20	2	10.0
11	18	3	16.6	16	4	25.0
12	19	4	21.0	20	4	20.0
13	14	1	7.1	12	2	16.6
15	20	3	15.0	19	4	21.0
24	20	4	20.0	10	1	10.0
26	20	5	25.0	17	4	23.5
28	19	3	15.7	17	5	29.4
35	17	2	11.7	19	2	10.5
36	17	6	35.2	20	5	25.0
45	16	6	37.5	20	4	20.0
48	15	6	40.0	20	3	15.0
52	16	1	6.2	15	2	13.3
53	18	8	44.4	18	2	11.1
55	14	4	28.5	14	1	7.1

TABLE A—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Susceptible F ₂ families						
10.....	20	18	90.0	17	17	100.0
16.....	20	17	85.0	15	12	80.0
17.....	18	18	100.0	17	11	64.7
30.....	18	18	100.0	19	14	73.6
33.....	18	18	100.0	20	17	85.0
41.....	19	19	100.0	18	14	77.7
42.....	18	18	100.0	19	17	89.4
46.....	20	20	100.0	20	17	85.0
54.....	19	19	100.0	16	16	100.0
Dissimilar reacting F ₂ families						
2.....	19	0	0	12	4	33.3
29.....	18	4	22.2	19	0	0
40.....	15	1	6.6	15	0	0
51.....	16	1	6.2	17	0	0

TABLE B

Results with F₂ Families of Hybrid No. 10 Descended from F₁ Plants which had been Inoculated with Ustilago Avenae

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F ₂ families						
106.	19	0	0	18	0	0
108.	19	0	0	20	0	0
111.	19	0	0	19	0	0
113.	16	0	0	18	0	0
122.	19	0	0	19	0	0
123.	15	0	0	19	0	0
127.	19	0	0	19	0	0
128.	20	0	0	20	0	0
129.	18	0	0	20	0	0
130.	18	0	0	18	0	0
132.	19	0	0	18	0	0
136.	16	0	0	17	0	0
137.	17	0	0	18	0	0
141.	17	0	0	15	0	0
145.	16	0	0	17	0	0
147.	19	0	0	17	0	0
151.	18	0	0	19	0	0
152.	14	0	0	18	0	0
154.	15	0	0	16	0	0
159.	14	0	0	16	0	0
160.	17	0	0	18	0	0
164.	18	0	0	19	0	0
167.	15	0	0	15	0	0
168.	18	0	0	18	0	0
170.	15	0	0	18	0	0
172.	16	0	0	16	0	0
173.	17	0	0	18	0	0
178.	17	0	0	19	0	0
181.	15	0	0	19	0	0
184.	12	0	0	18	0	0

Segregating F₂ families

109.	18	5	27.7	19	6	31.5
110.	19	3	15.7	18	2	11.1
112.	19	5	26.3	19	5	26.3
114.	17	4	23.5	17	3	17.6
115.	17	2	11.7	20	6	30.0
117.	16	6	37.5	20	5	25.0
118.	19	3	15.7	20	4	20.0
119.	20	7	35.0	18	5	27.7
120.	16	3	18.7	18	3	16.6

TABLE B—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.

 Segregating F₂ families—Continued

121.	20	5	25.0	17	3	17.6
124.	16	5	31.2	17	4	23.5
125.	18	3	16.6	19	4	21.0
126.	19	5	26.3	20	6	30.0
131.	20	4	20.0	13	2	15.3
133.	18	4	22.2	15	5	33.3
134.	15	3	20.0	16	3	18.7
135.	15	1	6.6	17	3	17.6
140.	12	1	8.3	14	3	21.4
142.	16	7	43.7	18	2	11.1
143.	18	4	22.2	17	7	41.1
144.	17	3	17.6	18	7	38.8
146.	18	6	33.3	16	2	12.5
148.	20	2	10.0	16	3	18.7
149.	18	8	44.4	18	3	16.6
150.	17	3	17.6	18	3	16.6
153.	14	7	50.0	20	7	35.0
155.	17	4	23.5	19	4	21.0
157.	14	2	14.2	17	6	35.2
158.	15	3	20.0	18	3	16.6
161.	19	2	10.5	17	2	11.7
162.	18	2	11.1	19	5	26.3
165.	16	3	18.7	17	1	5.8
166.	17	3	17.6	19	6	31.5
169.	17	2	11.7	20	3	15.0
174.	19	7	36.8	20	5	25.0
175.	18	6	33.3	15	4	26.6
176.	19	7	36.8	17	4	23.5
179.	18	4	22.2	14	2	14.2
183.	10	3	30.0	15	4	26.6

 Dissimilar reacting F₂ families

156.	16	0	0	18	1	5.5
177.	17	1	5.8	19	0	0
182.	16	4	25.0	14	0	0
107.	10	6	60.0	11	4	36.3
180.	17	9	52.9	20	4	20.0

TABLE C

Results with F₂ Families of Hybrid No. 10 Descended from F₂ Plants which had been Inoculated with Ustilago levis

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F ₂ families						
63.	17	0	0	18	0	0
72.	17	0	0	18	0	0
74.	18	0	0	11	0	0
76.	17	0	0	16	0	0
78.	17	0	0	18	0	0
85.	18	0	0	20	0	0
Segregating F ₂ families						
61.	20	5	25.0	18	2	11.1
62.	18	6	33.3	19	1	5.2
64.	18	7	38.8	19	3	15.7
65.	16	2	12.5	20	2	10.0
66.	19	4	21.0	18	3	16.6
67.	20	5	25.0	20	1	5.0
68.	20	7	35.0	16	4	25.0
69.	19	2	10.5	18	2	11.1
70.	16	2	12.5	12	2	16.6
71.	19	3	15.7	18	3	16.6
75.	20	6	30.0	20	5	25.0
80.	17	7	41.1	20	3	15.0
81.	19	4	21.0	18	4	22.2
84.	17	2	11.7	16	2	12.5
86.	20	2	10.0	19	5	26.3
87.	19	5	26.3	20	4	20.0
Dissimilar reacting F ₂ families						
82.	11	0	0	11	2	18.1
73.	18	6	33.3	10	0	0
79.	18	4	22.2	12	0	0

TABLE D

Results with F_2 Families of Hybrid No. 11 Descended from
Uninoculated F_2 Plants

F_2 Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F_2 families						
4	19	0	0	20	0	0
10	20	0	0	18	0	0
24	20	0	0	20	0	0
25	19	0	0	19	0	0
32	20	0	0	20	0	0
33	15	0	0	18	0	0
34	14	0	0	18	0	0
35	17	0	0	16	0	0
39	14	0	0	13	0	0
47	14	0	0	14	0	0
51	16	0	0	17	0	0
53	18	0	0	17	0	0
56	16	0	0	16	0	0
57	19	0	0	14	0	0
Segregating F_2 families						
1	19	3	15.7	17	6	35.2
2	20	2	10.0	20	2	10.0
3	19	6	30.0	16	4	25.0
11	20	5	25.0	17	3	17.6
14	20	5	25.0	20	3	15.0
18	20	4	20.0	20	8	44.4
19	18	3	16.6	20	5	25.0
21	20	10	50.0	20	7	35.0
22	15	3	20.0	19	2	10.5
28	19	6	31.5	18	3	16.6
29	19	4	21.0	17	4	23.5
36	17	4	23.5	19	1	5.2
38	15	3	20.0	15	3	20.0
41	19	7	36.8	17	2	11.7
43	18	8	44.4	16	5	31.2
44	14	3	21.4	16	1	6.2
45	19	3	15.7	18	3	16.6
48	13	4	30.7	15	7	46.6
49	18	3	16.6	16	1	6.2
52	15	4	26.6	18	3	16.6
58	15	6	40.0	17	1	5.8

TABLE D—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Susceptible F ₂ families						
12.....	20	16	84.2	16	10	62.5
15.....	19	17	89.4	19	19	100.0
26.....	20	15	75.0	20	13	65.0
31.....	20	18	90.0	18	17	94.4
42.....	16	15	93.7	13	10	76.9
50.....	15	13	86.6	17	13	76.4
55.....	17	16	94.1	18	11	61.1
Dissimilar reacting F ₂ families						
13.....	19	17	89.4	19	7	36.8
37.....	18	17	94.4	19	6	31.5
40.....	16	13	81.2	16	2	12.5
46.....	17	16	94.1	19	5	26.3

TABLE E

Results of F_2 Families of Hybrid No. 11 Descended from F_2 Plants which had been Inoculated with *Ustilago Avenae*

F_2 Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F_2 families						
110	17	0	0	18	0	0
112	18	0	0	18	0	0
114	15	0	0	19	0	0
115	18	0	0	19	0	0
118	11	0	0	16	0	0
119	19	0	0	18	0	0
121	17	0	0	20	0	0
126	11	0	0	18	0	0
127	16	0	0	18	0	0
128	13	0	0	19	0	0
130	16	0	0	18	0	0
132	15	0	0	13	0	0
135	16	0	0	17	0	0
137	17	0	0	15	0	0
144	13	0	0	18	0	0
146	15	0	0	12	0	0
151	16	0	0	17	0	0
156	14	0	0	17	0	0
157	17	0	0	16	0	0
158	15	0	0	14	0	0
159	17	0	0	16	0	0
160	12	0	0	16	0	0
183	16	0	0	17	0	0
186	13	0	0	16	0	0
Segregating F_2 families						
106	17	3	17.6	19	3	15.7
108	13	3	23.0	20	4	20.0
113	15	3	20.0	17	2	11.7
117	15	5	33.3	19	1	5.2
120	15	1	6.6	20	5	25.0
123	19	3	15.7	20	2	10.0
124	17	3	17.6	20	4	20.0
129	19	1	5.2	19	3	15.7
131	18	5	27.7	19	2	10.5

TABLE E—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.

Segregating F₂ families—Continued

134.	13	2	15.3	17	3	17.6
136.	18	7	38.8	17	2	11.7
138.	16	4	25.0	18	3	16.6
140.	17	5	29.4	17	2	11.7
142.	20	5	25.0	19	2	10.5
143.	17	3	17.6	17	3	17.6
145.	17	2	11.7	14	5	35.7
147.	15	4	26.6	18	3	16.6
148.	17	6	35.2	18	5	27.7
149.	15	2	13.3	16	3	18.7
150.	17	4	23.5	19	5	26.3
152.	18	5	27.7	18	1	5.5
153.	18	4	22.2	17	1	5.8
154.	15	5	33.3	19	2	10.5
155.	15	6	40.0	17	1	5.8
162.	17	2	11.7	18	3	16.6
164.	13	5	38.4	15	2	13.3
165.	11	4	36.3	17	3	17.6
167.	18	4	22.2	19	2	10.5
168.	18	3	16.6	18	3	16.6
169.	16	3	18.7	18	1	5.5
174.	16	4	25.0	16	1	6.2
175.	12	4	33.3	15	3	20.0
179.	17	6	35.2	16	3	18.7
180.	16	2	12.5	15	2	13.3
181.	18	5	27.7	16	3	18.7
182.	18	2	11.1	18	6	33.3
184.	16	2	12.5	14	3	21.4
185.	15	2	13.3	14	2	14.2

Dissimilar reacting F₂ families

116.	14	0	0	20	6	30.0
141.	15	0	0	19	6	31.5
171.	17	0	0	18	2	11.1
122.	18	1	5.5	19	0	0
125.	12	1	8.3	19	0	0
139.	18	4	22.2	14	0	0
163.	17	5	29.4	16	0	0
173.	17	4	23.5	15	0	0

TABLE F

Results with F_2 Families of Hybrid No. 11 Descended from F_2 Plants which had been Inoculated with *Ustilago levis*

F_2 Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F_2 families						
65.....	15	0	0	18	0	0
67.....	16	0	0	19	0	0
74.....	19	0	0	20	0	0
78.....	16	0	0	19	0	0
79.....	17	0	0	20	0	0
85.....	17	0	0	19	0	0
86.....	19	0	0	17	0	0
Segregating F_2 families						
61.....	19	5	26.3	18	4	22.2
64.....	18	5	27.7	20	8	40.0
66.....	20	7	35.0	20	6	30.0
68.....	20	5	25.0	20	4	20.0
69.....	20	6	30.0	18	2	11.1
70.....	20	6	30.0	20	3	15.0
71.....	19	3	15.7	19	4	21.0
72.....	20	6	30.0	19	3	15.7
73.....	17	3	17.6	20	7	35.0
75.....	17	5	29.4	19	4	21.0
76.....	20	5	25.0	20	6	30.0
77.....	19	4	21.0	19	6	31.5
80.....	17	3	17.6	20	2	10.0
82.....	18	4	22.2	19	2	10.5
84.....	19	4	21.0	19	3	15.7
Susceptible F_2 family						
62.....	19	19	100.0	18	11	61.1
Dissimilar reacting F_2 families						
87.....	18	0	0	19	3	15.7
63.....	20	3	15.0	18	0	0

TABLE G

*Results with F₃ Families of Hybrid No. 12 Descended from
Uninoculated F₂ Plants*

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F ₃ families						
1.....	17	0	0	18	0	0
2.....	17	0	0	19	0	0
8.....	16	0	0	19	0	0
9.....	16	0	0	20	0	0
10.....	17	0	0	20	0	0
15.....	19	0	0	20	0	0
26.....	18	0	0	20	0	0
30.....	12	0	0	14	0	0
36.....	15	0	0	18	0	0
37.....	16	0	0	10	0	0
40.....	15	0	0	13	0	0
47.....	14	0	0	13	0	0
56.....	15	0	0	18	0	0
57.....	16	0	0	15	0	0
Segregating F ₃ families						
3.....	19	3	15.7	19	4	21.0
4.....	18	3	16.6	19	4	21.0
7.....	20	3	15.0	19	1	5.2
12.....	12	1	8.3	19	5	26.3
16.....	19	1	6.2	20	4	20.0
18.....	16	2	12.5	20	5	25.0
21.....	14	1	7.1	20	1	5.0
23.....	18	4	22.2	19	3	15.7
24.....	18	2	11.1	20	1	5.0
25.....	17	3	17.6	20	2	10.0
32.....	17	2	11.7	18	5	27.7
35.....	17	5	29.4	16	1	6.2
41.....	19	5	26.3	13	3	23.0
44.....	19	5	26.3	15	4	26.6
46.....	16	5	31.2	16	5	31.2
49.....	16	5	31.2	16	4	25.0
51.....	16	2	12.5	17	3	17.6
54.....	13	4	30.7	14	1	7.1
55.....	13	1	7.6	15	1	6.6

TABLE G—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Susceptible F ₂ families						
17	15	15	100.0	20	14	70.0
27	10	9	90.0	20	10	50.0
38	18	17	94.4	18	11	61.1
43	18	18	100.0	15	12	80.0
45	20	20	100.0	20	19	95.0
50	15	10	66.6	15	9	60.0
58	16	16	100.0	17	14	82.3
Dissimilar reacting F ₂ families						
6	12	0	0	19	1	5.2
20	16	0	0	20	5	25.0
11	16	3	18.7	19	0	0
13	13	3	16.6	18	0	0
34	18	5	27.7	16	0	0
52	15	5	33.3	10	0	0
53	17	5	29.4	12	0	0
22	18	18	100.0	20	9	45.0
42	18	16	88.8	13	4	30.7

TABLE H

*Results with F₂ Families of Hybrid No. 12 Descended from F₂ Plants
which had been Inoculated with Ustilago Avenae*

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F ₂ families						
118.....	18	0	0	20	0	0
121.....	19	0	0	20	0	0
123.....	18	0	0	16	0	0
125.....	17	0	0	19	0	0
127.....	18	0	0	20	0	0
128.....	18	0	0	18	0	0
137.....	13	0	0	16	0	0
139.....	16	0	0	14	0	0
140.....	12	0	0	14	0	0
141.....	15	0	0	14	0	0
149.....	14	0	0	14	0	0
151.....	17	0	0	14	0	0
161.....	12	0	0	15	0	0
169.....	15	0	0	14	0	0
171.....	17	0	0	13	0	0
172.....	18	0	0	15	0	0
177.....	18	0	0	20	0	0
178.....	16	0	0	17	0	0
189.....	12	0	0	18	0	0
191.....	16	0	0	17	0	0
192.....	18	0	0	18	0	0

Segregating F₂ families

112.....	20	5	25.0	15	4	26.6
113.....	20	7	35.0	19	3	15.7
114.....	18	5	27.7	18	2	11.1
115.....	16	3	18.7	20	3	15.0
116.....	19	6	31.5	18	6	33.3
117.....	19	3	15.7	19	3	15.7
119.....	18	6	33.3	18	4	22.2
120.....	18	6	33.3	17	6	35.2
122.....	20	7	35.0	18	8	44.4
124.....	19	4	21.0	18	3	16.6
126.....	17	4	23.5	19	4	21.0
129.....	19	5	26.3	19	5	26.3
130.....	14	1	7.1	19	3	15.7
132.....	16	4	25.0	19	3	15.7
133.....	18	5	27.7	16	7	43.7
134.....	17	3	17.6	19	5	26.3

TABLE H—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.

Segregating F₂ families—Continued

135.....	18	4	22.2	18	5	27.7
136.....	15	2	13.3	17	3	17.6
138.....	15	1	6.6	17	2	11.7
142.....	15	6	40.0	18	4	22.2
143.....	13	4	30.7	17	5	29.4
145.....	15	4	26.6	18	2	11.1
146.....	17	8	47.0	18	3	16.6
147.....	14	2	14.2	14	2	14.2
148.....	12	4	33.3	15	5	33.3
150.....	19	7	36.8	18	3	16.6
155.....	15	5	33.3	18	4	22.2
156.....	10	1	10.0	15	1	6.6
159.....	12	5	41.6	12	1	8.3
160.....	16	2	12.5	17	1	5.8
162.....	19	5	26.3	18	5	27.7
165.....	15	2	13.3	15	6	40.0
167.....	18	4	22.2	16	1	6.2
173.....	18	3	16.6	13	1	7.6
174.....	12	4	33.3	12	5	41.6
175.....	17	1	5.8	15	3	20.0
179.....	19	8	42.1	19	5	26.3
180.....	16	2	12.5	17	6	35.2
181.....	19	6	31.5	15	1	6.6
182.....	13	2	15.3	13	2	15.3
183.....	19	3	15.7	16	3	18.7
185.....	14	4	28.5	15	5	33.3
187.....	17	4	23.5	17	2	11.7
190.....	14	2	14.2	14	5	35.7
193.....	16	4	25.0	13	2	15.3

Dissimilar reacting F₂ families

154.....	17	0	0	16	2	12.5
111.....	18	5	27.7	16	0	0
131.....	19	1	5.2	18	0	0
168.....	19	10	52.6	17	6	35.2

TABLE I

Results with F₂ Families of Hybrid No. 12 Descended from F₂ Plants which had been Inoculated with Ustilago levis

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F ₂ families						
69	19	0	0	20	0	0
70	17	0	0	19	0	0
78	19	0	0	19	0	0
83	19	0	0	18	0	0
86	20	0	0	17	0	0
Segregating F ₂ families						
61	19	3	15.7	18	5	27.7
62	19	3	15.7	20	2	10.0
65	16	3	18.7	20	1	5.0
66	18	5	27.7	19	2	10.5
67	19	5	26.3	20	6	30.0
71	20	4	20.0	17	1	5.8
72	17	4	23.5	17	5	29.4
75	19	7	36.8	19	1	5.2
77	20	4	20.0	19	5	26.3
80	19	5	26.3	18	3	16.6
81	20	7	35.0	18	2	11.1
84	16	3	18.7	20	4	20.0
87	18	6	33.3	16	2	12.5
91	19	5	26.3	19	4	21.0
Susceptible F ₂ family						
76	17	17	100.0	17	14	82.3
Dissimilar reacting F ₂ families						
68	18	6	33.3	19	0	0
73	18	2	11.1	20	0	0
82	19	2	10.5	20	0	0

TABLE J

Results with F_2 Families of Hybrid No. 13 Descended from
Uninoculated F_2 Plants

F_2 Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
2.....	17	0	0	14	0	0
4.....	16	0	0	17	0	0
5.....	17	0	0	17	0	0
23.....	15	0	0	14	0	0
34.....	17	0	0	16	0	0
40.....	16	0	0	16	0	0
41.....	13	0	0	14	0	0
43.....	15	0	0	14	0	0
45.....	15	0	0	15	0	0
50.....	17	0	0	17	0	0

1.....	17	4	23.5	16	2	12.5
3.....	18	4	22.2	14	5	35.7
6.....	17	4	23.5	16	2	12.5
7.....	13	4	30.7	17	7	41.1
11.....	18	4	22.2	17	6	35.2
13.....	18	3	16.6	16	4	25.0
18.....	18	6	33.3	14	4	28.5
19.....	15	3	20.0	17	3	17.6
24.....	16	2	12.5	12	1	8.3
28.....	18	6	33.3	19	9	47.3
33.....	14	2	14.2	11	2	18.1
35.....	19	5	26.3	14	2	14.2
36.....	16	2	12.5	11	4	36.3
38.....	15	2	13.3	14	4	28.5
39.....	13	3	23.0	15	4	26.6
42.....	16	3	18.7	15	4	26.6
44.....	16	8	50.0	14	5	35.7
49.....	17	3	17.6	20	6	30.0
51.....	17	6	35.2	18	3	16.6
52.....	16	3	18.7	13	6	46.1
53.....	18	2	11.1	15	2	13.3
55.....	15	5	33.3	16	5	31.2
56.....	16	5	31.2	20	1	5.0
59.....	16	7	43.7	17	7	41.1

TABLE J—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Susceptible F ₂ families						
9.....	15	14	93.3	19	17	89.4
12.....	17	17	100.0	20	19	95.0
17.....	18	16	88.8	16	11	68.7
25.....	18	16	88.8	14	13	92.8
27.....	20	17	85.0	16	16	100.0
29.....	18	18	100.0	18	17	94.4
31.....	18	18	100.0	18	15	83.3
32.....	18	16	88.8	16	14	87.5
37.....	15	14	93.3	13	11	84.6
46.....	18	16	88.8	13	13	100.0
47.....	17	17	100.0	17	16	94.1
54.....	17	17	100.0	15	15	100.0
57.....	17	15	88.2	17	9	52.9
58.....	20	20	100.0	16	16	100.0
Dissimilar reacting F ₂ families						
15.....	16	0	0	17	5	29.4
21.....	15	0	0	16	3	18.7

TABLE K

Results with F_2 Families of Hybrid No. 13 Descended from F_2 Plants which had been Inoculated with *Ustilago Avenae*

F_2 Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F_2 families						
101.....	13	0	0	15	0	0
102.....	15	0	0	14	0	0
105.....	15	0	0	12	0	0
108.....	15	0	0	18	0	0
110.....	17	0	0	17	0	0
116.....	10	0	0	11	0	0
120.....	14	0	0	16	0	0
122.....	11	0	0	16	0	0
123.....	14	0	0	17	0	0
125.....	16	0	0	18	0	0
129.....	13	0	0	17	0	0
130.....	10	0	0	16	0	0
133.....	18	0	0	18	0	0
146.....	11	0	0	18	0	0
147.....	15	0	0	17	0	0
148.....	16	0	0	15	0	0
156.....	14	0	0	19	0	0
167.....	13	0	0	16	0	0
174.....	11	0	0	19	0	0
175.....	13	0	0	18	0	0
179.....	16	0	0	17	0	0
180.....	13	0	0	18	0	0
185.....	15	0	0	16	0	0
Segregating F_2 families						
103.....	14	6	42.8	15	7	46.6
104.....	12	2	16.6	15	3	20.0
109.....	17	6	35.2	15	2	13.3
111.....	17	4	23.5	13	3	23.0
112.....	15	2	13.3	10	1	10.0
113.....	17	6	35.2	16	4	25.0
114.....	15	1	6.6	15	1	6.6
115.....	15	4	26.6	15	5	33.3
117.....	12	5	41.6	16	3	18.7
118.....	12	3	25.0	13	6	46.1
119.....	14	2	14.2	18	2	11.1
121.....	17	4	23.5	18	6	33.3
124.....	13	3	23.0	19	2	10.5
126.....	17	8	47.0	20	7	35.0
127.....	13	3	23.0	19	7	36.8
128.....	17	3	17.6	19	4	21.0
131.....	11	4	36.3	16	1	6.2

TABLE K—Continued

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago lenis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
132.....	17	4	23.5	15	2	13.3
134.....	14	4	28.5	18	4	22.2
136.....	14	6	42.8	17	1	5.8
149.....	13	4	30.7	16	4	25.0
151.....	16	7	43.7	15	5	33.3
152.....	14	1	7.1	16	4	25.0
153.....	14	4	28.5	16	4	25.0
154.....	15	3	20.0	15	4	26.6
155.....	10	3	30.0	16	4	25.0
157.....	16	7	43.7	18	5	27.7
158.....	18	3	16.6	19	3	15.7
159.....	13	3	23.0	16	6	37.5
160.....	12	2	16.6	19	5	26.3
161.....	10	4	40.0	20	2	10.0
163.....	10	5	50.0	18	3	16.6
164.....	13	4	30.7	18	3	16.6
165.....	14	5	35.7	16	5	31.2
166.....	15	4	26.6	18	7	38.8
168.....	12	1	8.3	19	4	21.0
169.....	11	2	18.1	18	5	27.7
170.....	12	3	25.0	15	3	20.0
171.....	12	2	16.6	18	5	27.7
172.....	10	3	30.0	18	8	44.4
173.....	10	4	40.0	18	3	16.6
176.....	11	2	18.1	17	3	17.6
177.....	14	7	50.0	17	5	29.4
181.....	10	4	40.0	16	3	18.7
182.....	15	4	26.6	14	2	14.2
183.....	13	4	30.7	16	3	18.7
184.....	13	5	38.4	19	4	21.0

Dissimilar reacting F₂ families

150.....	15	0	0	19	5	26.3
145.....	14	8	57.1	17	4	23.5

TABLE L

Results with F₂ Families of Hybrid No. 13 Descended from F₂ Plants which had been Inoculated with Ustilago levis

F ₂ Plant No.	Inoculated with <i>Ustilago Avenae</i>			Inoculated with <i>Ustilago levis</i>		
	No. Plants	No. Inf.	% Inf.	No. Plants	No. Inf.	% Inf.
Resistant F ₂ families						
61.....	15	0	0	15	0	0
65.....	16	0	0	16	0	0
69.....	15	0	0	13	0	0
71.....	19	0	0	15	0	0
73.....	17	0	0	17	0	0
83.....	19	0	0	13	0	0
90.....	16	0	0	15	0	0
Segregating F ₂ families						
62.....	18	4	22.2	19	7	36.8
63.....	19	5	26.3	14	6	42.8
64.....	14	4	28.5	18	5	27.7
67.....	18	4	22.2	16	3	18.7
68.....	18	6	33.3	17	4	23.5
70.....	18	2	11.1	14	4	28.5
72.....	17	1	5.8	16	3	18.7
74.....	18	2	11.1	14	2	14.2
75.....	16	4	25.0	14	3	21.4
76.....	15	3	20.0	16	8	50.0
78.....	18	5	27.7	16	5	31.2
79.....	17	2	11.7	17	5	29.4
81.....	16	1	6.2	16	4	25.0
84.....	18	3	16.6	13	4	30.7
86.....	19	1	5.2	14	7	50.0
88.....	17	1	5.8	15	3	20.0
89.....	17	2	11.7	18	3	16.6
Dissimilar reacting F ₂ families						
66.....	19	11	57.8	18	4	22.2

TABLE M

General Summary of Results with F_2 Families of Hybrids No. 10, 11, 12, 13—Hull-1088
(Seed No. 30) \times Black Mesdag (Seed No. 70)

I. F_2 families descended from uninoculated F_2 plants

Inoculated with <i>Ustilago Avenae</i>											
Resistant families						Segregating families				Susceptible families	
No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.
Hybrid No. 10 . . .	18	306	0	0	18	74	23.4	9	170	165	97.0
" " No. 11 . . .	14	241	0	0	21	96	25.8	7	127	110	86.6
" " No. 12 . . .	14	223	0	0	19	57	17.9	7	112	105	93.7
" " No. 13 . . .	10	158	0	0	24	96	24.4	14	246	231	93.9
Total	56	928	0	0	82	323	23.1	37	655	611	93.2

Inoculated with <i>Ustilago levis</i>											
No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.
Hybrid No. 10 . . .	18	309	0	0	18	50	16.5	9	161	135	83.8
" " No. 11 . . .	14	240	0	0	21	74	19.9	7	121	93	76.8
" " No. 12 . . .	14	237	0	0	19	57	17.0	7	125	89	71.2
" " No. 13 . . .	10	154	0	0	24	98	26.4	14	228	202	88.5
Total	56	940	0	0	82	279	20.2	37	635	519	81.7

TABLE M—Continued
 II. F₂ families descended from F₁ plants which had been inoculated with *Ustilago Avenae*

Inoculated with <i>Ustilago Avenae</i>									
Resistant families					Segregating families				
No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants
Hybrid No. 10. . . .	30	507	0	0	39	669	23 4		
" " No. 11. . . .	24	367	0	0	38	617	22 5		
" " No. 12. . . .	21	337	0	0	45	740	24 7		
" " No. 13. . . .	23	318	0	0	47	639	28 1		
Total	98	1529	0	0	169	2865	24 7		
Inoculated with <i>Ustilago levis</i>									
No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants
Hybrid No. 10. . .	30	539	0	0	39	685	22 6		
" " No. 11. . . .	24	405	0	0	38	663	15 6		
" " No. 12. . . .	21	346	0	0	45	751	21 5		
" " No. 13. . . .	23	378	0	0	47	783	23 3		
Total	98	1668	0	0	169	2882	20 9		

TABLE M—Continued

III. F₂ families descended from F₁ plants which had been inoculated with *Ustilago levis*

Inoculated with <i>Ustilago Avenae</i>									
Resistant families					Segregating families				
No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants
Hybrid No. 10.....	6	104	0	0	16	297	69	23.2	
" No. 11.....	7	119	0	0	15	283	71	25.0	
" No. 12.....	5	94	0	0	14	259	64	24.7	
" No. 13.....	7	117	0	0	17	293	50	17.0	
Total.....	25	434	0	0	62	1132	254	22.4	
Inoculated with <i>Ustilago levis</i>									
No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants	No. Inf.	% Inf.	No. Families	No. Plants
Hybrid No. 10.....	6	101	0	0	16	291	46	15.8	
" No. 11.....	7	132	0	0	15	290	64	22.0	
" No. 12.....	5	93	0	0	14	260	43	16.5	
" No. 13.....	7	104	0	0	17	267	76	28.4	
Total.....	25	430	0	0	62	1108	229	20.6	

^a Hybrid No. 11 F₂-62. ^b Hybrid No. 12 F₂-76. The appearance of these two families in the susceptible group is doubtless due to the failure to secure infection of the F₁ parent by covered smut.

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GEOLOGICAL RECONNAISSANCE OF PARTS OF GRAND, JACKSON AND LARIMER COUNTIES, COLORADO*

By L. E. SPOCK, JR.

CONTENTS

	Page
Introduction	178
Conditions of work and acknowledgments.....	178
Location and area	179
Previous geologic work.....	179
Relief and drainage.....	179
Geography and transportation.....	180
Outline of the geology.....	181
The Archean complex.....	182
Sedimentary rocks	182
Tertiary volcanics	183
Quaternary deposits	183
Descriptive geology and petrography.....	184
The pre-Cambrian rocks	184
Schist and gneiss.....	184
Resumé	195
Intrusive rocks	195
Sedimentary rocks	198
Paleozoic	199
Carboniferous	199
Permo-Triassic	199
Chugwater formation	199
Distribution, character and thickness.....	199
Stratigraphic relations	200
Cretaceous	200
The Niobrara (?) formation	200
The Pierre (?) formation.....	201
Sedimentary rocks of Middle Park.....	202
The Pierre.....	203
Eocene	203
The Denver formation.....	203
Distribution and general relations.....	203
Basal igneous beds.....	205
Conglomerates and sandstones.....	212
Fossils, age and correlation.....	213
Tertiary volcanic rocks	214

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Distribution and structural relations	214
Lava flows and tuffs	214
Rhyolites and associated types.....	215
Obsidian	217
Rhyolitic tuff	219
Porphyry Peaks rhyolite.....	221
Microspherulitic obsidian.....	223
Volcanic ash.....	226
Rocks of intermediate and femic composition.....	228
Basalt	231
Trachyandesite series.....	232
Intrusive rocks.....	236
Quartz monzonite porphyry.....	236
Granodiorite	240
Syenite porphyry.....	242
Igneous rocks of uncertain age.....	242
Granite porphyry	242
Geomorphology	244
Evolution of the present structure.....	244
Recent physiographic development.....	247
Glacial geology.....	250
Rivers and drainage.....	252
General surface features.....	255
Economic geology.....	256
Metals	256
Coal and hydrocarbons.....	258
Water resources	259
Bibliography	260

INTRODUCTION

CONDITIONS OF WORK AND ACKNOWLEDGMENTS

The material for this report was gathered during the summer of 1927. The work was undertaken in conjunction with an examination of prospects for the Happy Thought Mining Company of Gold Hill, Colorado. The traverses, which form the basis for mapping, were made on foot from a series of base camps encircling the area.

The writer is indebted to Messrs. B. P. Bailey, J. W. Kirkbride and M. W. Turner for supplying the means to carry on the work. Much aid and information were supplied by the inhabitants, to which limits of space forbid individual acknowledgment. Thanks are due to the members of the Faculty of the Geology Department of Columbia University for advice and suggestions in connection with the manuscript.

LOCATION AND AREA

Most of the area mapped lies in Grand County, but at the northern end a few square miles of Jackson and Larimer Counties are also included. It occupies the northeast corner of Middle Park and the adjacent part of the Continental Divide. The region lies between Willow Creek on the west and the North Fork of the Colorado River on the east. The Continental Divide forms the northwest boundary as far as Nokhu Crags. The area includes approximately 201 square miles. It is irregular in plan and is widest at the south, becoming narrower to the north. It lies between $105^{\circ} 50'$ and $106^{\circ} 13'$ west longitude and between $40^{\circ} 8'$ and $40^{\circ} 33'$ north latitude.

PREVIOUS GEOLOGIC WORK

The earliest geologic work performed in the area was that of the Hayden (14) and King (16) surveys.¹ The first geologic map was made by Marvine (20, pp. 154-192) of the Hayden Survey in 1874. The northern end of the area was briefly touched upon by the Fortieth Parallel Survey (13, pp. 94-129), in its account of the Medicine Bow Range and North Park.

In the years immediately following the early government surveys and until the advent of the "Laramie Problem," little work was done on the "Western Slope." As a result of the Laramie Problem the Mesozoic and Tertiary sediments were examined by Cross (6, p. 214). The most recent geologic mapping in nearby localities is that of Beekly (3) in North Park and that of Blackwelder (4, pp. 615-658) in the Medicine Bow Range. Although the area has never received detailed geologic study, it has been carefully examined for mineral occurrences, to which a great number of prospect holes bear witness.

RELIEF AND DRAINAGE

The country here described lies on the so-called "Western Slope," and embraces part of the Continental Divide known as the Never Summer Mountains. Here the Continental Divide swings away from the Front Range and follows a southwest-northeast course, along the ridge which separates North from Middle Park. The topography is rough and mountainous, the product of uplift followed by active fluvial and glacial erosion. The highest point is Mount Richthofen, 12,953 feet; the lowest

¹ Throughout this paper the bibliographical references are designated by an italicized number in parentheses. The author and title of the paper may be ascertained by referring to the corresponding number in the Bibliography.

elevation, 7,993 feet, is near Granby in the extreme south. This represents a maximum difference of a mile, but the average relief is considerably less.

Streams are plentiful everywhere. They belong to three main drainage systems. In the southeast the streams flow into the North Fork of the Colorado River. The rest of the drainage, south of the Continental Divide, flows into Willow and Stillwater creeks, which are tributaries of the Colorado. North of the Continental Divide the water flows either into the Middle Fork of Michigan Creek, which is on the west side of the Medicine Bow Range, or into Joe Wright Creek, tributaries of the North and South Platte rivers respectively. Most of these streams rise in the snow banks which remain in the higher and more protected places throughout the summer, and in the springs which derive their water from these snow banks. For this reason there is a continual supply of clear, cold water which is free from hardness. Much of the water is diverted from the Colorado and Michigan Creek drainage basins for agricultural purposes in the neighborhood of Fort Collins. Precipitation is heavy but variable on account of the relief.

GEOGRAPHY AND TRANSPORTATION

Although there are no towns within the area, Granby and Grand Lake are close by. Granby is a shipping and buying center for the ranchers south of the Continental Divide. Grand Lake is a summer resort and a point of interest for the tourists.

Transportation is supplied by the Denver and Rocky Mountain Railroad, which runs through Granby, and by state and county roads. These highways are constantly being improved and carry an ever-increasing amount of motor traffic. During the winter months, however, the roads are not open across the passes.

The chief industries are sheep-raising, cattle-raising and, to a less extent, accommodation of tourists. The ranches are located wherever the valley floor is sufficiently wide. These were taken under the Homesteading Act. The remaining land is part of the Arapaho National Forest and is open to grazing and lumbering only by arrangement with the Government.

Most of the area is covered by a thick forest of spruce, pine and aspen. The timber-line is remarkably constant at an elevation which seldom varies from 11,000 feet regardless of direction and exposure. Above this level, grass and weeds afford good grazing for sheep where the underlying rock is schist or gneiss. The mountains which are capped by

volcanics have little vegetation above the timber-line, since the rapid disintegration of the tuffs and flows yields little soil on the talus slopes below.

In the Willow Creek drainage basin many of the tributary valley floors are covered with sagebrush—a result of the barren sandstone soil rather than of climatic conditions. Sagebrush is rare where the underlying rock is other than sandstone.

OUTLINE OF THE GEOLOGY

For the purpose of description the rocks of the region may be separated into four groups as follows:

Quaternary deposits.

Tertiary volcanics.

Sedimentary rocks.

Archean Complex.

The general geologic section is given herewith:

SYSTEM	SERIES	FORMATION	CHARACTER
Quaternary	Recent		Alluvium and talus
	Pleistocene		Modified and unmodified glacial debris
Tertiary			Pyroclastics, lavas, and intrusive rocks
	Eocene	Denver formation	Arkose and conglomerate with andesitic base
Cretaceous	Montanan	Pierre shale	Fossiliferous shale and sandstone
	Coloradoan	Niobrara	Thin bedded calcareous shale
Permo-Triassic		Chugwater formation	Red shale and sandstone
Carboniferous (?)			Massive limestone exposed in fault block
Pre-Cambrian			Injection schist and gneiss with granite and rhyolite

THE ARCHEAN COMPLEX

This consists largely of hornblende and biotite schists and gneisses. Both types have been injected by magmatic juices so that no trace of their pre-metamorphic structure remains. The schists and gneisses grade into each other and cannot be differentiated. Their relations are so intimate that they must be treated as a single unit. They are cut by pegmatite dikes and quartz-bearing porphyries. In some places the magmatic attack has been so intense that the foliate rocks have been completely digested and replaced by a syntectic granite. The syntectic granite and its related dikes and veins have not been metamorphosed and therefore do not partake of the same diastrophic history as the schists and gneisses. There can be found every gradation between chlorite biotite schist and injection gneisses composed almost entirely of igneous material. The dips measured on the cleavage are uniformly steep. Those less than forty degrees are rare. No such uniformity governs the strikes, which may change as much as forty-five degrees in less than half a mile. Mountains which are made up of these pre-Cambrian rocks show the bold rounded pattern of topography which is so characteristic of schist and gneiss exposed to a moist climate. The rocks of the Archean Complex are largely concealed by younger rocks in the Willow Creek drainage basin. Elsewhere they, together with occasional volcanic capping, are exposed over the entire area.

SEDIMENTARY ROCKS

There are two distinct areas of sedimentary rocks in the region. In the Willow Creek drainage basin two formations are exposed. The older formation, the Pierre, outcrops at the mouth of Trail Creek, where it consists of sandstone and fossiliferous black shale standing at a high angle. Most of the drainage basin is occupied by beds of coarse sandstone and conglomerate of Eocene age, the equivalent of the Denver formation of the Denver Basin. The tuffaceous agglomerate base of the Denver formation overlies the Pierre unconformably. The only organic remains collected from it are abraded fragments of fossil plants. The structure of the Denver formation in Middle Park is that of an interrupted irregular basin. The Denver formation lies partly on the truncated Cretaceous sediments and partly on the pre-Cambrian crystallines. The topography produced from the sediments is characterized by mesas, cuestas and hogbacks.

In the vicinity of Cameron Pass sedimentary rocks are preserved in a series of narrow northwest-trending fault blocks. The formations

encountered are limestone probably of Carboniferous age, about 800 feet of the Chugwater (Permo-Triassic) red beds, a mashed fossiliferous portion of the Niobrara, and a graywacke phase of the Pierre formation. With the exception of the last named, which forms the vertical scarp of Nokhu Crag, they do not exert a marked control on the topography.

TERTIARY VOLCANICS

The Tertiary igneous rocks are present chiefly as lava flows and as beds of pyroclastic material. Intrusive rocks in the form of dikes and irregular bodies are present in the vicinity of Willow and Cameron passes. Both rhyolitic and basaltic rocks are common, but rocks of an intermediate type are also present, especially andesite. The lava flows cap nearly all the higher mountains, where they rest upon a pre-Cambrian base. However, other flows may be found at much lower altitudes. Consequently it is plain that the lavas were poured forth on a rough topography—a topography that is separated by a physiographic unconformity from the one of the present day. The vent or vents from which these lavas flowed have not been found in this area, but there is reason to believe that they came from the east. The volcanic history is not identical for the whole region. The differences relate to composition and sequence rather than to any fundamental difference in origin. The volcanics are easily disintegrated and are therefore characterized by vertical scarps and steep talus slopes.

QUATERNARY DEPOSITS

The Quaternary deposits include glacial drift, river gravels and talus sheets. It is not always possible to distinguish between these three types. At the higher altitudes, on both sides of the Continental Divide, intense local glaciation has carved out many cirques. In these rock basins unmodified moraines have been preserved; elsewhere the glacial drift has been reworked by vigorous streams to a normal river gravel. Erratics are rare, and not readily distinguished from the stream-borne boulders. River gravels have been deposited as flood plains by the Colorado and to a less extent by Willow Creek, and as alluvial fans by the tributaries of these streams. The flood-plain gravels are buried below a rich silt, which yields fertile meadows even where the country rock is a barren sandstone. Wherever volcanic rocks are found, the slopes below are buried beneath a thick deposit of coarse angular talus, obscuring alike the earlier glacial deposits and the bedrock. In the absence of volcanics the schists are covered by a thick residual soil.

The amount of recognizable moraine seems insufficient in comparison with the extensive glacial erosion. This discrepancy is more apparent than real and is caused not only by the post-glacial reworking of the drift, but also by its burial under talus in the over-steepened valleys.

DESCRIPTIVE GEOLOGY AND PETROGRAPHY

THE PRE-CAMBRIAN ROCKS

SCHISTS AND GNEISSES

The ancient metamorphic and igneous rocks of the area are continuous with, and essentially a part of, the crystallines which form the Front Range and the southern end of the Medicine Bow. The uplift of the complex in comparatively late geologic time has produced the ranges of the Rocky Mountains as we know them. Farther north in the Medicine Bow Mountains there are sediments of Algonkian age which have been described by Blackwelder (4, pp. 615-658). In this area, however, there are no formations recognizable between the Archean and the Carboniferous.

The most outstanding characteristic of the pre-Cambrian foliate rocks is their intense and complete metamorphism—a change so thorough that no direct evidence of their pre-diastrophic habit can be found. The metamorphism was brought about at considerable depth, in an environment of pressures and temperatures of sufficient magnitude to effect complete recrystallization of all the original constituents, and to impress on them the parallel structure of typical schist and gneiss. Although these rocks show little difference in degree of metamorphism, there exists a wide range of variability: of mineral composition, of texture, of attitude and of post-metamorphic igneous attack. Each one of these differences has an important bearing on the geologic history and will be discussed separately.

It is impossible to describe the metamorphic rocks apart from the igneous history which has been superimposed upon them. The magmatic attack took place in a very intimate and penetrating manner, with the result that the entire series has been soaked by injection material. Hence the rocks, with only minor exceptions, are injection schists and gneisses rather than simple metamorphics. The rising solutions, ascending from the magma chamber below, followed the cleavage planes and, upon precipitating their loads, have yielded rocks of a mixed type, in which bands of the metamorphic minerals alternate with bands of introduced material. It is impossible to assign a cause for *lit-par-lit* injection, which can

be demonstrated. Nevertheless, it seems probable that the attack was set in motion in response to the relief of pressure occasioned by uplift of the region in pre-Mesozoic time.

The metamorphic rocks include a complete series, of which one end is represented by simple gneiss or schist and the other by syntectonic granite of complex mineral composition. The nature of the series

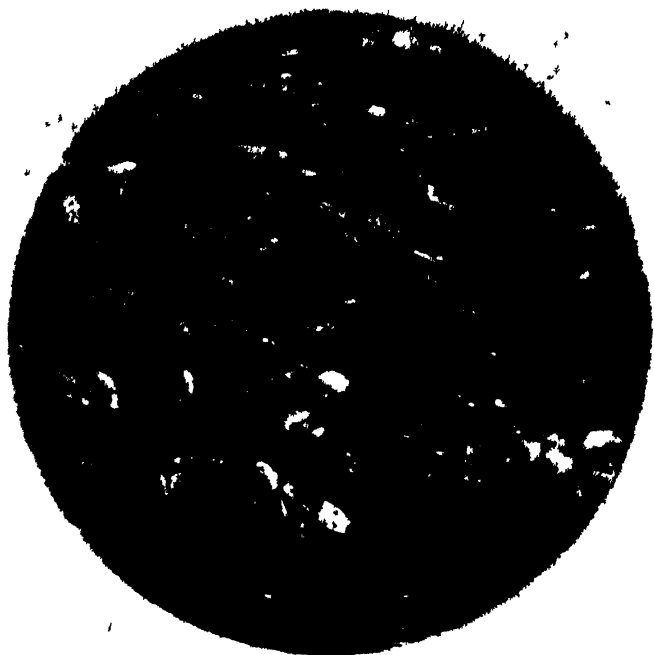


FIG. 2.—*Specimen B-5. Hornblende schist*

Plain light. Magnification $\times 30$. Taken to show the predominance of hornblende. The light-colored areas are quartz. This is the simplest of the metamorphic rocks.

is best explained by a petrographic study of the extreme and intermediate types.

The simplest type of foliate rock is a dark-green hornblende schist exposed on the Michigan Ditch, immediately east of Ditch Camp No. 1. This rock displays a moderately fine texture and a prominent, though slightly wrinkled, cleavage. It is unusual because of its simple mineralogy, and for the fact that of all the similar specimens examined it alone does not show evidence of igneous injection. The hornblende,

which comprises about three-fourths of the rock is a bright-green pleochroic variety, common in the region to the entire series of metamorphics. The hornblende crystals show a parallel orientation, which is nearly perfect, and they are remarkable for their accordance in size. With the hornblende there is present biotite of a shredded habit and interstitial arrangement. The other iron-bearing minerals are ilmenite and a chlorite which has been derived from the hornblende. Some quartz is present in small crystals. The remainder of the rock consists of a fine, nearly opaque, mixed aggregate which is markedly interstitial. Although the exact mineral composition of the aggregate cannot be determined, leucoxene and sericite are most abundant. There are no visible effects of subsequent stresses; the shredding and bending of the biotite seems contemporaneous with the final crystallization of the rock. The rock is classified as an amphibolite or hornblende schist.

The simplest of the mixed rocks is well illustrated by specimens from the south end of the Medicine Bow Range. These show a prominent banded structure, in which dark-green metamorphic minerals alternate with bands of pegmatite material. The structure is not produced by parallel mineral orientation. The average width of the bands is about a quarter of an inch; those more than six inches wide are uncommon. The texture of the metamorphic bands is moderately coarse, that of the pegmatite coarse but variable. The feature which is emphasized here is the simplicity of mineral composition. The only ferromagnesian mineral present in this rock is a bright-green pleochroic hornblende. This hornblende has not suffered chemical alteration during the injection, but is ragged and irregular in outline and has been broken by strains accompanying the salic constituents which have been introduced and those which represent recrystallization under the influence of regional metamorphism. It seems probable, however, in the light of further evidence that all the salic material has been introduced. The feldspars are all alkalic varieties: orthoclase, albite, albite-oligoclase and microcline. It is significant that the feldspars are heavily dusted with fine specks of sericite. This alteration is attributed to the final stages of igneous attack rather than to supergene decay. Since all the feldspar is attacked in this fashion, it seems very probable that none of this mineral belonged to the original metamorphic rock. It is apparent that, when first crystallized, the feldspar crystals were well formed and hypidiomorphic. This tendency toward regularity of outline has been largely destroyed by the later introduction of the quartz. Quartz constitutes about one third of the salic material. It was introduced after the feldspar. This is illustrated by its interstitial position and replacing habit. The distri-

bution of the quartz is scattered. It has formed small and irregularly shaped crystals which follow the margins of the feldspars and in part replace them. Inclusions of gas cavities are common in the quartz and form good evidence for their hypogene origin.

Post-igneous changes within the rock are slight. Strain shadows in the quartz and occasional bent feldspar lamellæ point to the presence of strains. Chemical alteration is confined to the formation of leucoxene and minor amounts of hydrated iron oxides. It is probable that all such alterations have taken place in response to the slow change of environment within the rock itself, as reactions toward a condition of internal stability, which no rock can ever attain.

At this point it is pertinent to inquire into the nature of the material of which this rock and those previously described represent the metamorphosed phase. Simplicity of mineral composition does not imply a corresponding simplicity of chemical composition. It remains to be found, on the basis of probability, what kind of common rock material may be integrated into mono-mineralic hornblende rock. From the composition of hornblende in general it may be deduced that the original rock was of a femic type. The integration of chlorite schists and similar rocks to hornblendites under the attack of introduced granite is well known. Schwartz (21, pp. 89-138) has discussed this problem at length and listed many examples.

A less completely integrated type of metamorphic rock having the same general history is illustrated by a specimen collected on the Medicine Bow Range, one mile south of the specimen just described. Although this rock resembles the other in general dynamic and igneous history, the structural arrangement is somewhat different. In contrast to the definite banded structure of the specimen described above, it shows megascopically only an obscure orientation of the ferromagnesian minerals. These minerals, hornblende and biotite, are large, and only oriented in one dimension. They have the appearance of being scattered irregularly through the matrix of introduced material, and occasionally show a patchy or aggregate distribution. In the hand specimen it resembles a sheared granodiorite rather than a metamorphic rock. Under the microscope this similarity to an igneous rock becomes even more marked. The texture is coarse and distinctly granitoid, and the crystals are interlocked. The femic minerals consist of hornblende, biotite, chlorite, ilmenite and garnet. Of these, the first two are most abundant and seem to be the critical minerals. Garnet and ilmenite are present in minor amounts as distinctly metamorphic products. The salic constituents are quartz, orthoclase, albite, albite-oligoclase and apatite. Subsequent

hypogene alteration of the feldspar has been intense. This igneous attack has followed the cleavages and margins of the feldspar, producing dense aggregates of sericite, carbonates and saussurite. The quartz is present rather as a normal igneous mineral than in the metasomatic relationship shown in the first specimen. Post-igneous changes include the alteration of some of the ilmenite to leucoxene, and of feldspar to carbonate. Since the rock consists about two-thirds of introduced salic



FIG. 3.—*Specimen L-29-a. Injected hornblende schist*

Plain light. Magnification $\times 30$. This rock is similar to the preceding, except in that this shows injection by quartz and alkali feldspar (the light-colored areas).

minerals, and one third of femic minerals, which are only in part metamorphic, it is difficult to classify. This is either a syntectic granodiorite or else an injection gneiss. Actually, the specimen represents one of the steps in a complete gradation which exists between the hornblende and the biotite. The thin section shows hornblende partly changed to biotite as one of the steps in the reaction series which Bowen (5, p. 177) postulates for igneous melts. However, it is not possible

to differentiate between the ferromagnesians which belong to the metamorphic history and those which have been introduced. One explanation immediately suggests itself. It is quite possible that the original metamorphic mineral is the hornblende and that, as a result of the attempt of the invading magma to reach a stable phase, the hornblende has been reworked to a biotite identical in composition with the biotite crystallizing from the magma. The uniform character of the biotite and



FIG. 4.—Specimen E-25. Injection gneiss from Medicine Bow Range

Plain light. Magnification $\times 30$. Note the ragged margins of the hornblende and the intimate penetration of the silic constituents. The clear areas are quartz.

the change from biotite to chlorite both suggest that this may be the actual solution. The general bending and shredding of the biotite in the absence of strain effects on the quartz indicate stresses which accompanied, rather than followed, the introduction of the magmatic material.

A more advanced stage of injection is displayed in the vicinity of the Wheeler Ranch, section 7 T. 5 N., R. 77 W. Specimens from this lo-

cality possess a strong parallel banded structure in which wide streaks of introduced quartz alternate with thin films of metamorphic minerals. These are present in ratio of about six to one. The hornblende, common to all the metamorphic rocks, has been completely made over to biotite, chlorite and magnetite, so that no trace of its structure remains. The biotite has retained its parallel orientation although it has been violently shredded and bent. The introduced material consists of quartz with a

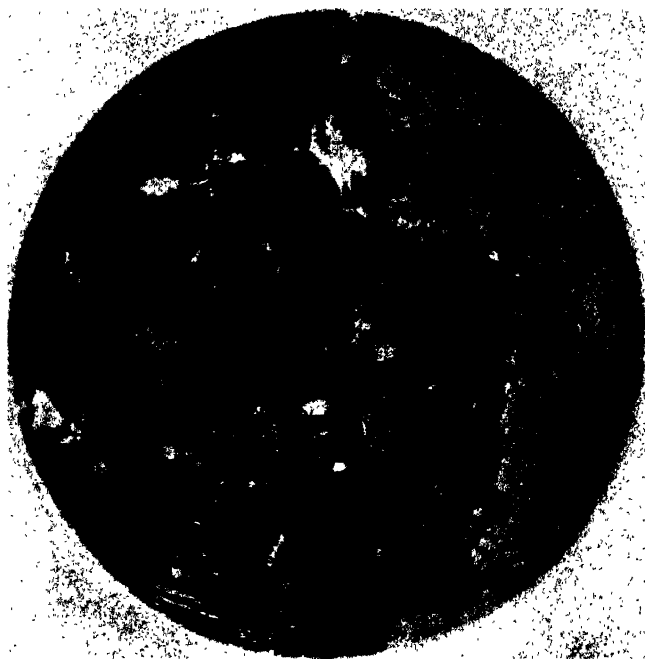


FIG. 5.—*Specimen C-19. Infection gneiss*

Plain light. Magnification $\times 30$. Note the resemblance to the granitoid structure of igneous rocks. The darker patches are serpentine. The rough gray areas are altered feldspar.

small proportion of microcline. The quartz crystals are large and irregular. They are surprisingly free from strain shadows, but deformation is displayed by the mosaics of broken quartz and bent twinning lamellæ of the microcline. The igneous attack illustrated here shows some noteworthy differences when compared with those already described. We see in this specimen introduction of quartz vein material

instead of injection by pegmatite and granodiorite juice. The effect has been to produce a more complete invasion of the rock. This is manifested by the wide spreading apart and deformation of the metamorphic foliæ and by the breaking down of the hornblende. The intensity of the attack and the large amount of material introduced are doubtless the result of the superior mobility and penetrating power of



FIG. 6.—*Specimen M. Injection gneiss*

Plain light. Magnification $\times 30$. Note the shredded habit and parallel orientation of the biotite. The light-colored areas are largely vein quartz with only minor amounts of feldspar. It is believed that this specimen represents the most advanced type of lit-par-lit injection.

the quartz vein material in comparison with those emanations which theoretically belong to the earlier stages of magmatic history.

Contrasted with the last four rocks, there frequently occurs a type having the same minerals but an entirely different structure. This type is well represented by the material from the vicinity of Supply Creek at the Arapaho Forest boundary. This specimen shows a coarse and highly variable texture, together with the massive interlocked struc-

ture of plutonic rocks. Megascopically it resembles quartz diorite or quartz monzonite. In the field it grades into injection schist on all sides, a change which takes place by the acquisition of foliation rather than a change of minerals. The feldspars consist of orthoclase and zoned alkalic plagioclases, which have suffered a mild hypogene attack. Quartz comprises about five per cent of the rock. The femic minerals are hornblende, biotite, chlorite and titanite, and the accessories are garnet,



FIG. 7.—*Specimen L-4-D. Syntectic granodiorite*

Plain light. Magnification $\times 30$. Note the massive plutonic character of this rock. There is no suggestion of foliate structure and yet the minerals are the same as those of the gneisses.

ilmenite, magnetite and apatite. The critical points, however, are these: the hornblende has been partly changed to biotite and the biotite to chlorite. With one exception the colored minerals are of precisely the same color and optical behavior as those already described in the other rocks. In addition to this similarity there are many patches of alteration products which mark the position of completely replaced and

digested hornblende crystals. These show the outline or pattern of the cleavage though the mineral itself may be completely destroyed. There are two kinds of biotite present in the rock. One is the pale variety, also found in the specimens from the Medicine Bow, and which belongs to the metamorphic history. The other biotite is darker, the typical biotite found in granites. All these criteria point to one conclusion: that this rock is a syntectic, produced through intimate mix-



FIG. 8.—*Specimen L-26-B. Syntectic granite*

Plain light. Magnification $\times 30$. Taken to show the granitoid structure common to the syntectic rocks. The dark area is hornblende which has gone over to biotite. Note the alteration of the feldspar.

ing and partial digestion by magmatic juices attacking and reworking metamorphic rocks of a basic composition.

In the same vicinity, that is, west of the Colorado River from Bowen Gulch south to Stillwater Creek, the syntectic granites are more abundant than the foliate rocks. The granites vary considerably in texture and outward appearance, but their mineralogy and petrographic history

are everywhere the same. The most conspicuous features common to all the granites are the presence of the hornblende inherited from the foliate rocks, and the products of its incomplete digestion. Another similarity which is constant throughout the series is the later igneous history of the granites. This is manifest in the strong sericitization of the feldspars, especially those of a sodic composition, and the late interstitial margin-forming habit of the quartz. It is as though the melt which produced the granites had been particularly rich in the mobile end-stage fluids.

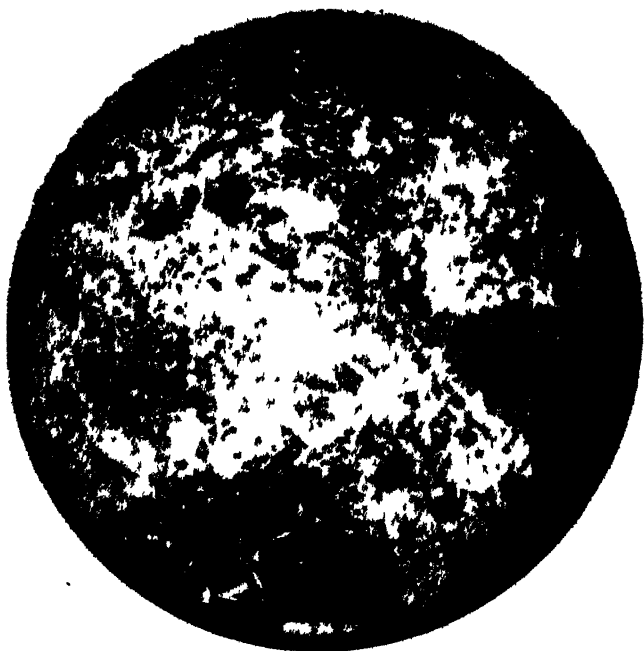


FIG. 9.—*Specimen L-37-a. Pegmatite with partially digested schist*

Plain light. Magnification $\times 15$. Note the garnet cut by fracture. The light-gray material is chlorite made from biotite. The light patches are quartz and feldspar.

Farther west on Blue Ridge, Mount Bennay, and Pony Park the effect of the end-stage fluids is even more noticeable. In addition to the granite there is present rock which is not so much syntectic granite as a syntectic pegmatite mass. In this material the foliate rocks have been less uniformly digested than is the case with the granites. Hence they appear as dark streaks of irregular shape in the pegmatite matrix.

Such "pegmatite," or coarse granite, consists essentially of pink orthoclase in large (2-4 mm.) but fairly regular crystals, together with much intergrown and interstitial quartz. Occasionally there is a slight development of tourmaline and garnet, but usually the minerals present are restricted to normal orthotectic species.

RÉSUMÉ

The entire pre-Cambrian series of the region is judged to have been formed by the method outlined above. The original formations of the region consisted of a series of ancient basic rocks, which were little different from the Archean tuffs and flows known in the pre-Cambrian shield as "Greenstones." Slight differences, no doubt, existed in composition and structural habit. Such variations are feebly reflected in the textures of the present complex rocks. The chief differences, however, are the result of the variable intensity of igneous attack; invasions by normal granite magma have produced one type of mixed rock, whereas pegmatite and end-stage emanations have given rise to others.

In certain localities rocks covering a large area are composed almost entirely of pegmatite. The original metamorphic rock in such places has been so thoroughly replaced that the only remnants are dark streaks and inclusions. Here the pegmatite does not occur as dikes but rather as formless bodies of extremely coarse, friable granite. This peculiar rock is found only in the higher mountains and it is possible that such places may lie immediately above cupolas in the batholithic mass below.

INTRUSIVE ROCKS

In addition to the igneous material which has mingled with and partly replaced the foliate rocks, there exists a series of intrusives of later age which have cut the schist and gneiss. The later igneous rocks are sometimes present as dikes, more often they form irregular masses. While the intrusives are younger than the syntectic granites just described, they are, nevertheless, older than the Tertiary volcanics. In the absence of widely distributed Paleozoic sediments in the area, it is impossible to date them precisely. Since they are confined to the pre-Cambrian rocks in their distribution, however, and act with them as a unit, they are treated as part of the pre-Cambrian series. Their relationships are best seen in the cuts which have been made in excavating for the Michigan Ditch one mile south of Cameron Pass. At this locality there is exposed an ancient erosion surface, which bevels the schist and intruded dike, and over which has been poured a Tertiary

obsidian flow. Although the intrusives vary considerably in texture and structure, they may all be grouped together as quartz or rhyolite porphyry.

The quartz-bearing porphyries are best exposed in the vicinity of Cameron Pass, but they also occur south of the Continental Divide. It is probable that the porphyries are just as common south of the Divide as they are farther north, but they are more often concealed by vegetation.

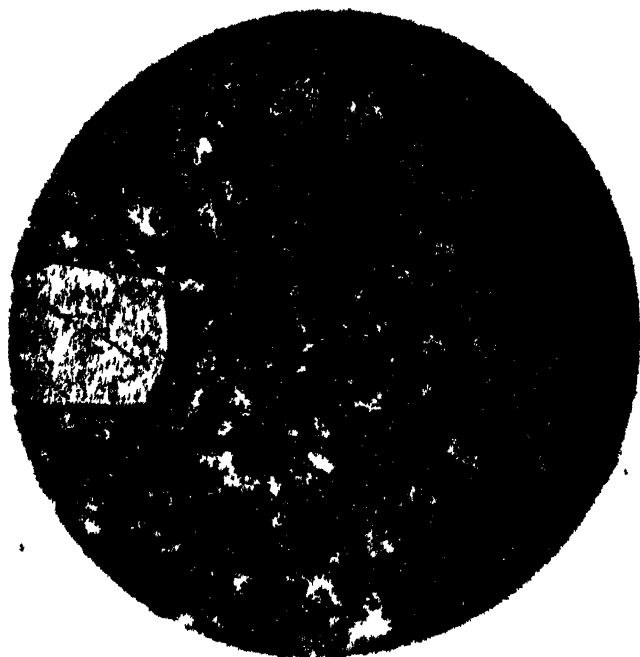


FIG. 10.—*Specimen B-7. Rhyolite porphyry exposed by Michigan Ditch*

Plain light. Magnification $\times 30$. Taken to show both idiomorphism and resorption of the sanidine phenocrysts. Note the two generations of minerals comprising the groundmass.

A striking example of the more salic porphyries is a rhyolite which has been exposed immediately east of Camp No. 1 on the Michigan Ditch. This dike, which cuts the schists almost parallel to its cleavage, is very light-colored and resembles aplite in the hand specimen.

The most prominent mineral in the rock is sanidine. The sanidine

crystals show strongly idiomorphic outlines under the microscope, and almost perfect Carlsbad twins. There are also idiomorphic phenocrysts of quartz present. Both the quartz and feldspar phenocrysts have suffered magmatic corrosion. The groundmass shows a fine variable texture, as though it consisted of material of two distinct generations. The coarser part of the groundmass is made up of irregularly shaped quartz crystals from 1 to 2 mm. in diameter. They are imbedded in an

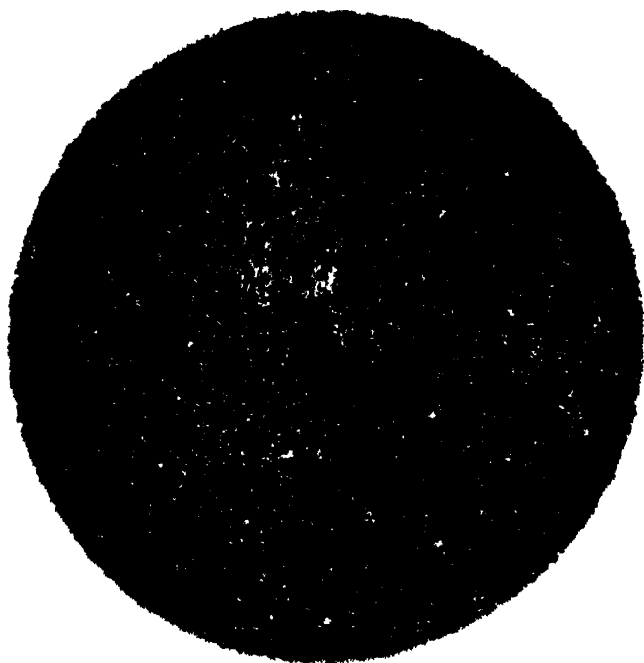


FIG. 11.—*Specimen L-34. Dellenite from Bowen Gulch*

Pl in light. Magnification $\times 30$. Note the obscure trachytic arrangement of the groundmass and the alteration of the feldspars.

extremely fine matrix of quartz and feldspar which probably represents a devitrified glassy groundmass. The only indication of feldspar constituents are a few scattered threads of altered biotite and irregular patches of hydrated iron oxides. Sericite is abundantly scattered through the groundmass, but it is impossible to tell whether it is a product of the devitrification, of subsequent weathering or of crystallization resulting from imprisoned gases.

A different type of intrusive porphyry is found near the abandoned mine six miles from the state road up Bowen Gulch. It occurs rather as an irregular mass than as a dike. It consists of large idiomorphic feldspar phenocrysts imbedded in a dense green groundmass. The feldspar phenocrysts are in part normal idiomorphic orthoclase and in part glassy sanidine. Both types show rectangular cross sections and zoned margins. Carlsbad twins are common. The groundmass consists of slender lath-like feldspars of a more salic composition, which show a somewhat obscure trachytic arrangement. The rest of the groundmass consists of magnetite, chlorite and carbonate. Quartz is present in minor amounts. The alteration of this rock has been intense; of the feldspar phenocrysts little remains but a dense aggregate of carbonate and sericite. In the groundmass the feldspar laths have been less affected, although there is much interstitial carbonate. This carbonate, the chlorite and the finely disseminated magnetite no doubt represent a product of the decomposition of some pre-existing ferromagnesian, now completely destroyed. This rock is best classified as a quartz-bearing trachyte porphyry or as a dellenite.

SEDIMENTARY ROCKS

The sedimentary rocks of the area occur in two separated localities, Cameron Pass and the Willow Creek drainage basin. Since the structural relations and, with one exception, the age of the sediments are different in these two localities, they may be most conveniently treated as two distinct units.

In the vicinity of Cameron Pass the sediments have been preserved only as isolated graben. The studies of Lee (18, p. 287) have shown that during Mesozoic time the area now occupied by the Southern Rockies was a site of deposition. Consequently the rocks found here, or their equivalents, must have covered the entire region. With the exception of the down-faulted blocks the section has been entirely removed by erosion from the region about the Divide. The members may be studied in their true relations, however, in North Park.

The graben mentioned are narrow troughs, with a general northwest trend, parallel to the strike of the beds which have dropped into them, parallel also to their exposures in North Park (8, Pl. XII) where their sedimentary contact with the Archean has been exposed. The date of this faulting cannot be set precisely, nevertheless it is earlier than the intrusion of the Tertiary volcanics by which the sediments are cut. It would be reasonable to expect them to have been formed in closing

Cretaceous time, as a result of the diastrophism of the Laramide Revolution.

PALEOZOIC

CARBONIFEROUS

Limestone of Carboniferous age outcrops only in two places: at the bend of the State Road where it turns west, 4,000 feet south of Cameron Pass, and on the crest of the Medicine Bow Range in section 27, T. 7 N., R. 76 W. This limestone is light gray, fine-grained and massive. It is traversed by joints and calcite veins. No fossils were found, nor was any bedding observed. For these reasons and because outcrops are small, the only evidence that can be employed for identification is its stratigraphic position. At both localities it is adjacent to a massive red sandstone, the Chugwater, which in each instance stands vertical. The actual contact is nowhere exposed. It is here correlated, tentatively, with the limestone described by Beekly (3, p. 21) in North Park, on the basis of lithology, stratigraphic probability and stratigraphic position. On account of its instability under atmospheric attack it is eroded more rapidly than the rocks on either side, namely, schist and sandstone. Consequently its exposures are soon buried, so that its relations to the sediments with which it has been down-faulted, and to the country rock, are rendered obscure.

PERMO-TRIASSIC

CHUGWATER FORMATION

Distribution, character and thickness.—The Chugwater sandstone outcrops at the two localities given for the Carboniferous limestone. It is also exposed, though poorly, in section 9, T. 6 N., R. 76 W., on the state road, and in the southeast quarter of section 11 of the same township. At both localities the rock has been preserved by down-faulting. The outcrop in section 9 is in a trough parallel to the first two, whereas the outcrop in section 11 is in an offset portion of the main down-faulted block at the bend in the state road. At the last-mentioned locality the outcrop can be detected only by the float. The structure is completely obscured. In section 11 about 800 feet of the Chugwater is exposed, but this probably does not represent its entire thickness. In general it is a friable ferruginous sandstone, but it shows considerable variation. The bottom beds are so thoroughly cemented as to give it the appearance of a quartzite and these beds are thick and massive. Higher in the formation the beds become thinner, more shaly, less competent, and less homo-

geneous. There is also a corresponding variation in the composition. When freshly broken, the lower beds are buff-colored and turn red only after exposure to the atmosphere. Above the quartzitic beds the buff sandstone becomes friable. In the upper part of the formation the content of both iron oxide and calcite increases. For this reason the shaly layers are of brilliant red color and contain occasional partings of nearly pure hematite and calcite. Calcite veins also cross the structure, following the joints, and thereby yield a structure which resembles bedding. Some of the higher beds are extremely fine-grained. The formation contains no fossils. Only one bedding plane shows ripple marks and these are wide-spaced and shallow. The strike of the sandstone is parallel to the trend of the graben, that is N. 62° W. The dip is variable as a result of drag; at the road it averages 60° W., but on the mountain-side, 800 feet above, the beds are vertical. In consequence of its high structure the sandstone is rapidly weathered by mechanical agencies and presents an extremely steep slope to the south. The iron-rich beds in the upper part weather down to a peculiar bright red clay which contains little sand and which dries out to a hard compact mass.

Stratigraphic relations.—The Chugwater formation is best exposed in section 11, where it lies between the Carboniferous limestone already described and a dark calcareous shale of Cretaceous age, which is probably the Niobrara. Its identification as the Chugwater is based on its similarity in position and lithology with the Chugwater as described by Beekly (3, pp. 23-26) in North Park. Darton (10, p. 397) defined the Chugwater to include the red beds between the Tensleep sandstone and Sundance formation. On account of its fault contacts, it is impossible to give the age of this formation, or part of a formation, more closely than is expressed by the term "Permo-Triassic."

CRETACEOUS

THE NIOBRARA (?) FORMATION

In the graben in section 11 where the Chugwater is exposed, there occurs adjacent to the Chugwater a dark-gray fine-grained calcareous shale. This formation has been so shattered that its bedding cannot be determined. A false appearance of bedding is imparted by parallel, epigene calcite veins. Although it contains many fossils, they are too poorly preserved for certain identification with the exception of one species of Foraminifera which is present in large numbers. This is *Gümbelina globulosa* (Ehrenberg).¹ The most abundant of the macro-

¹ Identified by Dr. H. N. Corryell.

fossils is a small bivalve about an inch long, which occurs in clusters. The irregular outline of these shells and their distribution are strongly suggestive of *Ostrea congesta*. In addition there are many fragments of some large molluscan shells, made up of transverse prisms. The prisms have a maximum length of 10 mm. The surface of the shells shows a distinct crenulate form, and to it are attached many of the smaller shells described above. The size and form of the shell and of the prisms give the fossil a decided resemblance to *Inoceramus deformis*. It is on the slender paleontologic evidence outlined above that the correlation is made. The Morrison is the formation one would expect above the Chugwater. Apparently the Morrison, the Dakota and the Benton have been cut out by the fault. On the opposite side of Michigan Creek, in the southeast extension of the graben, the Niobrara is exposed in several poor outcrops. No estimate can be made of its thickness. In the bed of the Michigan Creek where the graben has been cross-faulted, only two feet of the shale remain. Its thickness on the Cameron Pass Road, although not determinable, would be measured in hundreds of feet.

THE PIERRE (?) FORMATION

In addition to the Niobrara, there is one other Cretaceous formation outcropping in the vicinity of Cameron Pass. Its exposure forms part of the western scarp of Nokhu Crags, overlooking Lake Agnes, in section 14. The outcrop is inaccessible and can be studied only from the talus slope below, and from the general appearance of the scarp. Furthermore, its structural relations are hidden by talus and glacial deposits. However, from its position and from the structure in the vicinity, it seems more than probable that the formation has been dropped into one of the series of parallel graben common to the area. Its high topographic expression is a result of its resistance to erosion, occasioned by its massive structure and induration.

The rock is a drab sandy shale, highly indurated and traversed by many joints. Its disintegration into the coarse blocks forming the talus is largely a result of frost action. The rock is fine-grained and somewhat variable in composition. Some specimens are made up almost entirely of small, sharply angular quartz fragments bound together by dark indurated clay. Other specimens consist largely of clay, with but minor quantities of quartz fragments. The rock is remarkable for the uniform sorting of the clastic particles. It could best be classified as an indurated silt, such as is characteristic of deltas. The only fossil found in it is a species of *Inoceramus*. This organism is poorly preserved, but

closely resembles *Inoceramus cripsi* var *barabini*. The presence of the single genus *Inoceramus* is not sufficiently diagnostic by itself to place the rock in the time scale more closely than upper Cretaceous. The lithology and stratigraphic expectability, however, point strongly to its being an outlier of the Pierre shale of North Park, with which it is here tentatively correlated.

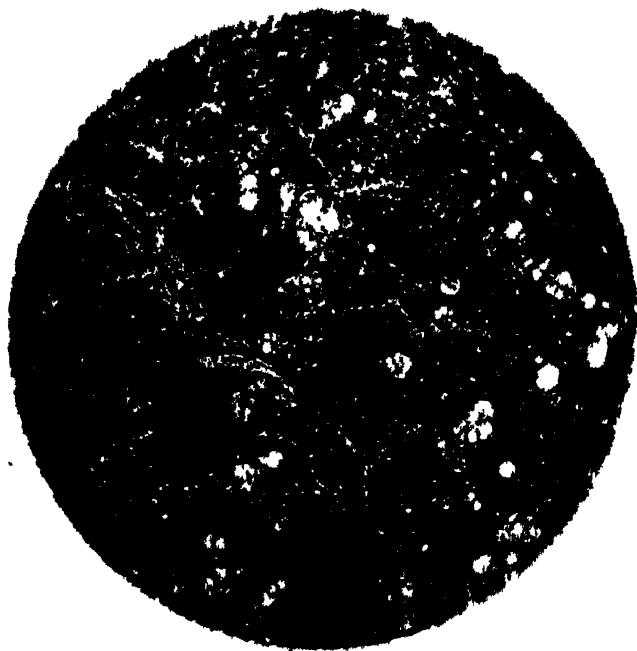


FIG. 12.—Specimen F-1. Fossiliferous shale (Niobrara)

Plain light. Magnification $\times 30$. Taken to show the abundant Foraminifera, *Gumbellina globulosa*. The streaks which cut the bedding are calcite shell fragments.

SEDIMENTARY ROCKS OF MIDDLE PARK

The second group of sedimentary rocks occurs in the Willow Creek drainage basin on the western side of the area. They consist largely of sandstone and conglomerate with interbedded igneous material. The formations involved are of upper Cretaceous and lower Eocene age. The sediments overlie the pre-Cambrian and are of sufficient thickness to conceal completely the metamorphic and igneous rocks below. The formations represented here are: a member of the Pierre and a thick sandstone

series, the equivalent of the Denver beds of the east side of the Front Range. There is an angular unconformity between the two.

The Pierre. The Pierre outcrops on the north side of the valley of Trail Creek, section 34, T. 3 N., R. 77 W. At this locality it emerges from below the basal tuffs of the overlying formation by which it is concealed in other parts of the region. The beds strike N. 50° E. and have a variable dip to the north. Two kinds of sedimentary material are present: an upper layer of sandstone and a lower series of dark shale. The sandstone is massive and resistant so that its outcrop presents a vertical scarp to the south. It is composed of fine sand particles cemented by calcite. Solution of the cement results in a honeycomb type of weathering which resembles the solution effects on massive limestone beds. The lower part of the exposure consists of a black shale which rapidly disintegrates to black clay at the surface. In the shaly beds the following fossils occur:

Inoceramus barabini

Scaphites nodosus var *quadrangularis*

Baculites compressus

There is also a small gastropod present which has not been identified. Although this faunule is sufficient to indicate the Pierre age of the formation, it is not sufficiently diagnostic to date the beds any more closely. The unconformity below the overlying beds has been discussed by Cross in his study of the post-Laramie beds of Middle Park. This unconformity was first noted at Windy Gap (6, p. 214), five miles south of the above locality. The deformation of the strata below the unconformity points to orogenic movements in late Cretaceous time, orogenic movements which took place either before or during the deformation of the Laramide Revolution. The presence of these beds was noted by Marvin (20, p. 172) in the Hayden Survey of 1873. They are correlated by him as part of "Cretaceous No. 5" or Fox Hills. Although he mentions the presence of fossils, no faunal list is given by him.

EOCENE

THE DENVER FORMATION

Distribution and general relations. The beds described in the preceding paragraph are overlain unconformably by a thick series of sediments and igneous material. With the exception of the outcrop of Pierre, already noted, no sedimentary rocks have been exposed by erosion below the Denver beds in the area here discussed. Where the contact can be found, the Denver beds lie directly on the ancient crystallines. The

distribution of the formation coincides roughly with the area of the Willow Creek drainage basin east of the Blue Ridge and Mount Bennay, and it continues northward into North Park, including Parkview and Radial mountains on the Continental Divide. The total thickness of the Denver Formation is approximately 5,000 feet.

The basal part of the formation consists of about 500 feet of igneous material: modified agglomerate, tuff and lava flow. Above the igneous material the beds show every gradation from fine sandstone to conglomerate with four-inch boulders.



FIG. 13.—Hogback formed by massive sandstone layers of the Pierre formation at the mouth of Trail Creek

The outcrop in the background is 30 feet high.

In general the dips are steep, although they change rapidly within short distances. On the east side of Gold Run the lower sandstone beds dip 55° N. W., on the north side of the same creek the dip is 45° . A few miles north of Gold Run the beds become nearly horizontal although the flat structure is interrupted by local anticlines. Immediately south of the Continental Divide the high structure is resumed, with dips directly away from the divide as high as 40° . Thus the Denver beds of this part of Middle Park form a definite though interrupted structural basin.

The variations in structure and lithology of the formation exert a marked control on the topography. The basal igneous material and conglomerate beds are relatively resistant to weathering and erosion. Consequently they form prominent cuestas and hogback ridges which in some instances can be traced for several miles. Often the development of such forms is so perfect that the back slope is a true dip slope. The sandstone beds yield more readily to stream abrasion than to weathering. As a result, valley widening lags behind downcutting, so that the outer valley walls in horizontal structure are usually vertical and canyon-like. The control of the Denver formation on drainage will be discussed with the physiography.

Basal igneous beds. The basal part of the Denver formation, consisting of femic igneous rock types, has already been briefly described by Marvine (30, p. 156), who named it the "Doleritic Breccia," and also by Cross (6, p. 200) and (8, pp. 214-216). It is best exposed in the ridge which forms the divide between Gold Run and Trail Creek. Other outcrops occur to the southwest of Trail Mountain. Its most northern exposure is the ridge in sections 13, 23, and 24, T. 4 N., R. 77 W. At this locality it is considerably thinner than farther south. There is no evidence that this may have formerly continued into North Park. No mention of it is made in Beekly's (3) recent report on that district and it is likely, in view of its rapid thinning, that the igneous beds would pinch out within a few miles. From the map it can be seen that its northward continuation has been removed by erosion.

The material of this basal portion shows a wide variability of both composition and structure. The lower part consists of pebbles and boulders, cemented by tuffaceous material. The upper part consists of intermingled tuff and lava flow. In the lava flow an irregular pillow structure can be observed. The pillows are separated by streaks of impure gypsum. The boulders at the base, although unsorted as to size, are arranged in definite beds from one to ten feet thick. The shape of these boulders varies between angular and well-rounded forms and shows evidence of some transportation by water. The largest boulder observed was four feet in diameter; however, boulders more than two feet in their largest dimension are uncommon. The matrix which binds the large fragmentals together is a dark indurated tuff of which the components show little evidence of transportation. Above the more massive igneous deposit the tuffaceous fragments are intermingled with the arkosic debris of the sandstone. Igneous pebbles similar to the lower boulders also occur with the gneissic pebbles in the conglomerate for several hundred feet up in the section. Hence the change from the pyroclastic beds

to the sandstones and conglomerates is transitional. Although the igneous rock types vary considerably in mineral composition, texture and structure, they show marked resemblances in many ways and there is no doubt that they all came from the same igneous source. The most outstanding types are briefly described below.

The most common rock type represented in the boulders of the lower beds is a pyroxene andesite. This usually occurs as large subangular

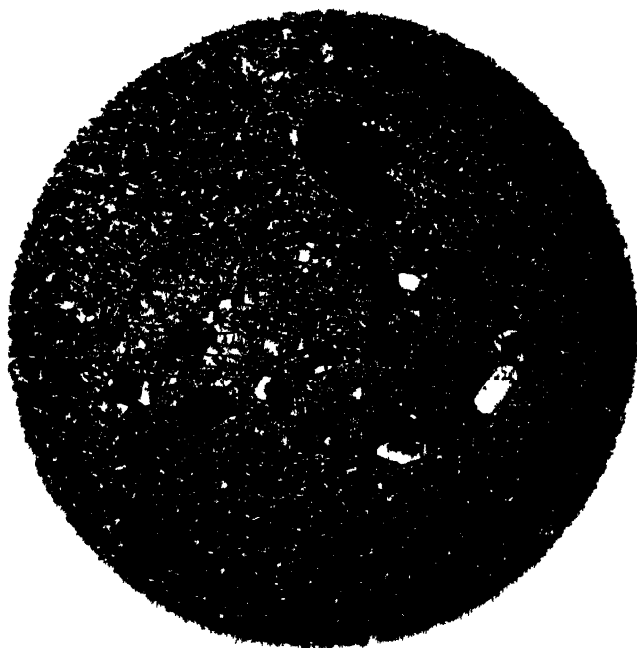


FIG. 14.—*Specimen J-12-a. Pyroxene andesite from the base of the Denier formation*

Plain light. Magnification $\times 30$. Taken especially to show the diabasic structure of the groundmass. Note the inclusions in the augite phenocryst. The well formed colorless crystals are apatite.

boulders, remarkably free from weathering effects. In color it is dark greenish gray, liberally sprinkled with black phenocrysts of augite. The groundmass is fine-textured and displays a prominent ophitic structure. The groundmass consists of microlitic laths of oligoclase of an intermediate composition. In addition there are formless patches of dark serpentine, grains of apatite and magnetite, and shreds of chlorite and epidote. Much of the groundmass is a complex aggregate produced by

the alteration of a femic glass, which has an interstitial arrangement with respect to the oligoclase laths. The altered glass consists essentially of serpentinous matter. The augite phenocrysts are large and strongly idiomorphic; in the hand specimen they appear jet black, in thin section they are pale green and nonpleochroic. They are uniform in size and in distribution. Their average length is between 3 and 4 mm. Magnetite, feldspar and apatite in crystals up to .2 mm. are abundantly present as irregularly distributed inclusions. There are a few isolated phenocrysts of feldspar remaining, which show a more calcic composition than the groundmass feldspar and belong between labradorite and bytownite. Nearly all the feldspar phenocrysts have suffered an attack in which they have been largely converted to serpentine and chlorite with smaller amounts of epidote. Most of the feldspars are surrounded by a selvage of more acid plagioclase. Magnetite is present as formless phenocrysts of different sizes. Apparently these were formed early in the crystallization history, for many of them have been broken and the fractures healed by the inflow of the groundmass material.

In comparison with the boulders described above there occurs another type, of a similar igneous history but with an entirely different mineral composition. This somewhat unusual rock is a porphyritic analcite basalt, which is common as small boulders in the outcrop west of Trail Mountain, in section 2, T. 2 N., R. 77 W. The groundmass is irregularly ophitic, its texture medium, but the size of the feldspar laths is highly variable. They grade from microlitic laths .05 mm. in length to phenocrysts nearly 2 mm. long. In composition the feldspar is uniform. It is an andesine-labradorite. It is twinned after the albite law, but the twinning lamellæ show a somewhat wedge-like splintering habit. Zoned margins are common. The groundmass further consists of magnetite grains, small augite crystals, grains of apatite, and dense drab-green aggregates of serpentinous material. This aggregate has an interstitial distribution which is strongly suggestive of an altered glassy matrix. The pyroxene phenocrysts are exactly the same pale green non-pleochroic augite observed in the previous specimen. However, they are more abundant in the analcite basalt, less regularly distributed and more variable in size. In the augite the schiller structure is not prominently displayed. Of chief interest in this specimen is the presence of analcite phenocrysts, which, like the augite, are strongly idiomorphic and of different sizes. Their diameters range from small fractions of a millimeter up to 3 mm. They are perfectly isotropic and remarkably free from inclusions. Although very little chemical alteration has taken place, the analcite is everywhere traversed by cracks and fissures, which

for the most part have been filled by chlorite and the serpentine-chlorite aggregate.

Another isometric mineral is present in such small quantities as not to be determinable. Phenocrysts of this substance may be measured with a diameter up to 1 mm.; however, all but extremely minute fragments have been replaced by carbonate. The isometric outline is preserved by heavy reaction rims of serpentine and chlorite. This mineral



FIG. 15.—*Specimen of J-12-B Analcite basalt*

Plain light. Magnification $\times 30$. Note the large analcite crystals and the irregular ophitic groundmass.

is readily visible in the hand specimen as minute spherical masses of a bright orange color. The color is a result of streaks of inclusions irregularly distributed. The remaining phenocrysts consist of the larger feldspar laths, magnetite and minor amounts of apatite.

The lowest portion of the volcanic series consists, not of a series of boulders or reworked agglomerate beds but of a true tuff which has not been modified by fluvial transportation. The tuff is made up almost

entirely of igneous rock fragments of diverse sizes. The fragments may be so small that several may be included in the same microscopic field 2 mm. in diameter. The larger fragments are several centimeters long. Ophitic structure and lath-like idiomorphism of the feldspars are common to all the fragments, although there is a wide diversity in the amount of feldspar and in the size of the crystals involved. In occasional patches the ophitic structure has been modified by flowage.



FIG. 10.—Specimen J-12-B. *Analcite basalt*

Through nearly all the types the same augite described in the two preceding rocks is freely distributed, either as large phenocrysts or else as a constituent of the groundmass. Nearly all the rock types represented in this tuff are devitrified femic porphyries. The devitrification is clearly of two distinct types, as shown by the condition of the iron oxides which have crystallized from the groundmass. Many of the lithic fragments are so freely sprinkled with magnetite grains that the groundmass is almost opaque; other fragments show instead of magnetite the red-colored particles typical of hydrated ferric oxides.

The fragments which show the incipient magnetite crystals have been devitrified in response to the unstable condition of the glass, as a result of the change of environment produced by cooling, without atmospheric attack. On the other hand, devitrification under the oxidizing conditions of the atmosphere has produced hematite or limonite in those fragments which retained their glassy condition after extrusion.

The contacts between fragments in most instances is sharp and well defined. Nevertheless, there are occasional boundaries in which two dissimilar types merge into each other by imperceptible degrees. This, no doubt, is produced by reorganization (mainly devitrification) of substances having the same composition, proceeding in the same direction and at the same speed. All the fragments observed can be classified as augite basalts. The differences relate to texture and degree of reorganization, and not to any fundamental difference of composition or petrologic history. These fragments contain the same augites, serpentine, feldspar, the same habit of magnetite and apatite displayed by the boulders already described.

A thin layer of actual lava forms the upper portion of the basal igneous series. This rock is more salic in appearance than the boulders and tuff fragments previously described. It is a light-colored gray-green rock in which phenocrysts and matrix are present in almost equal amounts. The groundmass is fine grained, though its texture is somewhat variable from place to place. Constituents of the groundmass are feldspar and chlorite, both of a shredded habit, and fine specks of magnetite. These are present as minute particles in a still finer aggregate composed of the same minerals. This aggregate owes its composition and structure to the breaking down of the original glassy matrix. The phenocrysts are feldspar and badly altered pyroxene and olivine. Feldspar crystals with a composition approximating oligoclase-albite are most abundant and comprise nearly forty per cent of the rock. They have strongly idiomorphic rectangular outlines which show neither resorption nor selvages. The largest feldspars are 1.4 mm. long. During the later igneous history these feldspars have been almost entirely changed to chlorite and saussurite, but the alteration has not affected their perfect rectangular outline, although the twinning lamellæ have been obscured. Some of the least altered feldspars show antiperthitic intergrowths. The augite phenocrysts have been partly altered to carbonate, to serpentine and to mixed aggregates of which serpentine is the most prominent mineral.

Of the minerals comprising this rock the unaltered pyroxene alone bears a strong resemblance to the constituents of the fragmental rocks

below. Of the olivine nothing remains but the orthorhombic outline, since it has been converted to a dense serpentinous aggregate. Weathering has produced minor amounts of hydrated ferric oxides. The lava is decidedly more acidic than the agglomerate and tuff. Furthermore, its structure shows the following differences: there is no suggestion of ophitic arrangement of the feldspar; the feldspars are strongly tabular rather than lath-like; they have suffered more severe alteration, and they

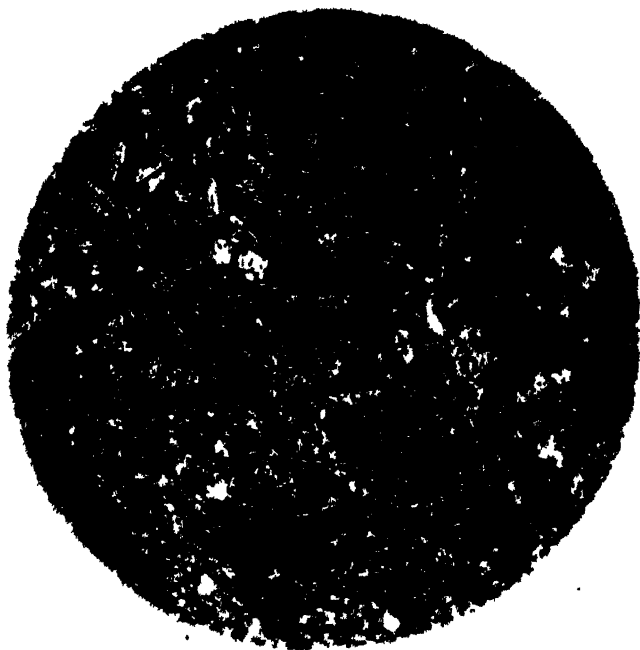


FIG. 17.—*Specimen J-12-C. Tuff at base of Denver formation*

Plain light. Magnification $\times 30$. Note the ophitic structure in the lithic fragments.

comprise a greater percentage of the rock. This last feature is one to be emphasized, for the phenocrysts of feldspar are large and closely crowded together. Like the fragmentals the lava shows a complete devitrification of the groundmass. It can best be classified as an augite andesite porphyry.

The source of the pyroclastics described above is not known. Beds containing lithologically similar material have been described by Cross (8, pp. 201-206 and 311-316) in the Denver formation of the Denver

Basin. In the same description suggestions are advanced as to the distribution of the areas covered by the volcanic rocks in question. However, in Middle Park the igneous material is more abundant than in the Denver Basin; it contains also lava flows and larger boulders. Furthermore, the amount or thickness of the volcanics increases to the southwest. For these reasons it seems probable that the eruptions which gave rise to the flows and clastics will be found to the west or southwest beyond the boundary of the area included in the report.



FIG. 18.— *Specimen J-1. Lava at base of Denver formation*

Plain light. Magnification $\times 30$. Taken to show the closely packed idiomorphic feldspar phenocrysts.

Conglomerates and sandstones. The beds above the basal igneous strata consist of indurated sands and gravels. Some pyroclastic fragments occur in the lower beds, where they may be found either singly or as small tuff lenses, but nearly all the debris has been derived from the pre-Cambrian crystalline rocks. Several distinct lithologic types are present, as well as every gradation between these types. The coarsest

rock of the series is a grayish-pink conglomerate which forms the sharp ridge to the northwest of Gold Run. It is composed of well rounded boulders and pebbles, which for the most part are pink injection gneiss, granites and pegmatite. The pebbles average about an inch in diameter, the largest exceed four inches in their greatest dimension. The finer material consists largely of angular quartz and orthoclase fragments. The minerals, whether present as separate fragments, or as components of the rock pebbles, are remarkable for their freshness. The arkosic character continues through the entire formation. The most abundant rock type is an impure buff-colored arkose. Its texture is naturally variable, but most outcrops contain fragments with a maximum diameter of 1.5 mm. The components are chiefly quartz and feldspar, but there is in addition a large amount of fresh muscovite. Usually the grains are poorly sorted and show different degrees of rounding in the same specimen. An unusual feature seen in several outcrops of arkose along Willow Creek is the occurrence of lenses of ilmenite sand. Such lenses, although seldom individually thicker than an inch, usually occur closely spaced, and are separated by thin partings of the lighter constituents. Apparently they represent indurated placer deposits of the heavier minerals, dropped where the former river currents were slackened. The change in texture of the sediments is abrupt, the sorting incomplete, and much of the material is angular or subangular. These characteristics, as well as the freshness of the feldspar and mica, point to conditions of rapid erosion and short transportation. Furthermore, the plant remains are preserved as broken fragments of leaves and wood. Usually they are found piled irregularly together as though they had been accumulated in the slack eddies of a rapid stream. In fact, all the descriptive details enumerated in this paragraph point to fluvial deposition by vigorous streams.

Fossils, age and correlation. The only organic remains found in these beds are fragments of plants. In the lower part of the formation pieces of silicified wood occur in which the structure of the plant has been well preserved, but it is not present in sufficient quantity to enable identification. The most abundant vegetable remains consist of closely packed abraded leaves, in which both outline and structure have been totally destroyed.

The formation here correlated with the Denver beds is one termed "Lignitic" by Marvine (20, p. 156). In his description, however, the basal igneous portion was not included as part of the formation. In spite of the lack of paleontologic evidence, the correlation of this formation with the Denver beds of the Denver Basin does not seem open to

serious questioning. Although lithologic similarity and succession are not often reliable bases for correlation, the similarity between the two series is of such a nature as to justify such a method in this case. Both formations immediately overlie an angular unconformity; each begins with a series of tuffaceous beds of unusual igneous rock types; and furthermore the igneous material, though variable, shows the same kind of pebbles and boulders in both formations. Likewise the upward transition from femic igneous pebbles to the gneissoid pebbles derived from the pre-Cambrian series is the same in both cases. Cross (6, p. 214) and (8, pp. 203-204, 214-215) has noted the similarity in two papers. In the Denver Basin the Denver formation, together with the Arapahoe, lies unconformably above the Laramie. Consequently the correlation of the Denver formation has been involved in the general problem of the "Laramie." It is not within the province of this report to inquire into the evidence for the age of the "Laramie" and "post-Laramie." The age of the Denver formation has been ably discussed by Cross (6, p. 214), (7, pp. 27-31), (8, pp. 206-254) and (9, pp. 27-45) in a series of papers in which the different lines of evidence have been carefully weighed. These are summarized by him (9, pp. 42-45) in his most recent paper on the subject, in which he urges their reference to the Eocene.

TERTIARY VOLCANIC ROCKS

DISTRIBUTION AND STRUCTURAL RELATIONS

The latest series of igneous rocks shows more variety of occurrence, composition and internal structure than the other volcanic rocks of the region. Furthermore, there is no apparent interrelationship demonstrated in their mineralogy or petrographic history. In the northeast and southeast areas, lava flows and igneous fragmental rocks cap nearly all the higher mountains. Contrasted with this series of variable extrusive rocks, a number of prominent uniform quartz monzonite porphyry dikes outcrop on the Continental Divide on either side of Willow Pass, where they cut through the Denver formation. Other intrusive rocks of irregular form and irregular distribution have invaded the sediments and crystallines in the vicinity of Lake Agnes. The distribution of the different igneous rock types is shown on the map.

LAVA FLOWS AND TUFFS

The following igneous rock types are represented among the lava flows: rhyolite of several varieties, including also porphyritic obsidian and spherulitic rhyolite, basalt, trachyandesites and andesites of scori-

aceous, amygdaloidal and glassy habit. With the lava flows are intercalated tuff beds and agglomerate of corresponding rock types. Although the fragmentals usually occur in the later stages of the igneous series, they are not confined to this position and occasionally occur with the basal flows. Except for the amygdaloidal andesite, which has a wide distribution in the southeastern part of the area, the lava flows are somewhat limited in their lateral extent and in most cases cannot be traced across intervening valleys. Also the succession of lava flows differs from place to place. The bottom member of the series is in some instances basalt, in others rhyolite or obsidian. The difference in the order of flows is the result of the limited horizontal extent of the rocks involved. In other words, the lava flows were formed as a series of imbricating lenses rather than as a succession of sheet-like flows. There is no progression in composition to show either increasing or decreasing basicity. The latter is well illustrated to the east of Cameron Pass on Lulu Mountain, where basaltic flows are "sandwiched" between two dissimilar rhyolites.

A feature important in the physiographic development of the area is the absence of accordance in altitude shown by the basal contacts of the lava flows. In the Cameron Pass region the discordance in altitude amounts to nearly a thousand feet. Apparently the lavas were poured forth over a land form of high relief. The present topographic expression of the lava flows is generally uniform, although subject to slight modification arising from texture and structure and to differences resulting from fluvial or glacial erosion. Usually the lava flows take the form of prominent mesas or gently dipping cuestas surrounded by steep escarpments and bare talus slopes. The sharpness of these forms has been accentuated in the higher altitudes by glacial features such as cirques and arêtes. In general the tuffs yield more rapidly to erosion and consequently do not show such marked topographic forms.

RHYOLITES AND ASSOCIATED TYPES

The largest rhyolite flow is that which caps Lulu Mountain east of Cameron Pass. This flow has a maximum thickness of 900 feet and forms a mesa which covers approximately five square miles. It dips gently to the northeast and presents a steep escarpment to the southwest. In the hand specimen the rock is pink and shows a prominent flow structure. The flowage lines are frequently interrupted by gas cavities about which pneumatolitic alteration has taken place. The groundmass is a fine, dense, interlocked aggregate consisting mainly of quartz and alkaline feldspar. Scattered through this aggregate there

are fine grains of magnetite, incipient crystals of green ferromagnesian, isolated flakes of muscovite and minute patches of hydrated iron oxides. The quartz and feldspar are arranged in irregular rosettes and spherulitic structures, which are closely interlocked and imbricating and which have been formed by the devitrification of the groundmass. There is a small amount of interstitial glass. The texture of the groundmass shows considerable variation; it is relatively coarse along the flow lines



FIG. 19.—*Specimen aaa. Rhyolite lava flow from Lulu Mountain*

Plain light Magnification $\times 60$. Note the resorption of the orthoclase phenocrysts. The zone of coarser texture which passes between the phenocrysts is a flow line. Its coarse texture has been produced by imprisoned gases.

and about the cavities, an effect which has been produced by the attack of escaping gases. The phenocrysts consist of clear fresh orthoclase. While most of these are either euhedral or subhedral, many have been corroded by resorption, so that their outlines present bold flowing curves. The feldspars, though unaltered, show many fractures, which have in most instances been healed by groundmass material. The phenocrysts have a maximum length of 3 mm. Their average maximum dimension,

however, is about 1 mm. The flow structure is marked by the coarser textures of the groundmass and by the primary deformation of the immediately adjacent groundmass into a series of roughly parallel drag folds. The rock owes its pink color to the finely disseminated specks of ferric oxides.

OBSIDIAN

Contrasted with the devitrified rhyolite described above, there outcrops a fresh porphyritic obsidian in section 12, T. 6 N., R. 76 W., which



FIG 20.—View of Lulu Mountain facing northeast

Taken to show the almost horizontal rhyolite flows Note the alternation of escarpments and talus slopes

has been exposed in cutting the Michigan Ditch. This obsidian rests directly upon an erosion surface which bevels the pre-Cambrian gneiss and pegmatite. The rock is a very dark-green glass with a strong primary flowage structure and abundant sanidine phenocrysts. The groundmass consists of highly salic rock glass. The glass is made up of alternate bands produced by flowage, which follow a wavy, undulating but essentially parallel course across the rock. These bands are sometimes crumpled into folds and sometimes deviate to curve about a phenocryst. The main part of the groundmass is composed of glass which is filled with the incipient crystals (trichites), showing the very earliest stage

of crystallization. The bands consist of glass which is free from or sparsely sprinkled with crystallites. The phenocrysts are of sanidine resorbed to rounded outlines. They are seldom larger than .75 mm. in diameter. Except for a slight alteration which follows the fractures and surrounds an occasional gas cavity, the rock is entirely fresh. This rhyolite in contact with the crystallines represents the first phase of Tertiary volcanic history for this particular locality.

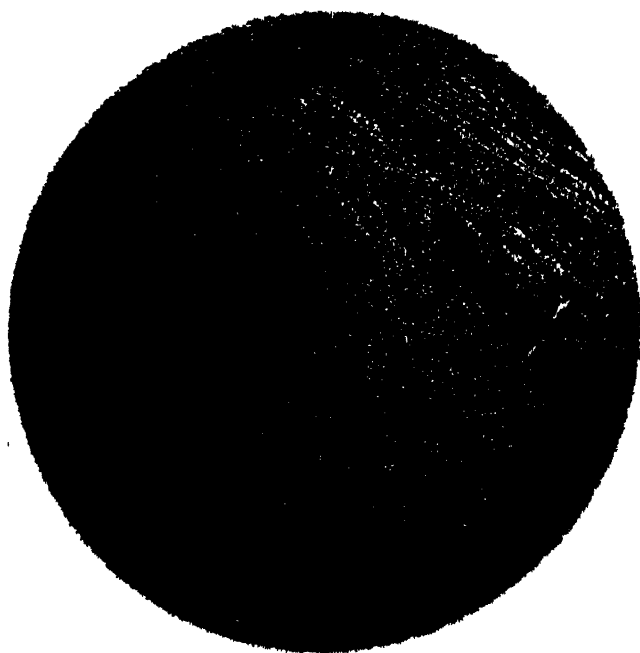


FIG. 21—*Specimen B-3. Obsidian*

Plain light. Magnification $\times 30$. Taken to show the flow banding and resorbed feldspar.

Associated with the obsidian just described there is another glassy rock with the same general composition, but which shows a more complex history. It differs from the preceding in that it is made up of black glass spherules interspersed with stony material. The flow structure is prominent, wavy and irregular. The glass matrix shows more recrystallization and is less salic than the more massive obsidian just described. Embedded in the matrix there appear not only the frac-

tured resorbed orthoclase phenocrysts, but also lithic fragments and fragments of the glass itself. Hence it is clear from the contained material that this rock is in part pyroclastic and in part enterolithic. In other words, this represents a glassy flow containing mingled fragments of its own cooled and fractured crust as well as foreign materials of a volcanic nature. The phenocrysts are alkali feldspar, biotite, muscovite and some resorbed ferromagnesians. The lithic fragments are

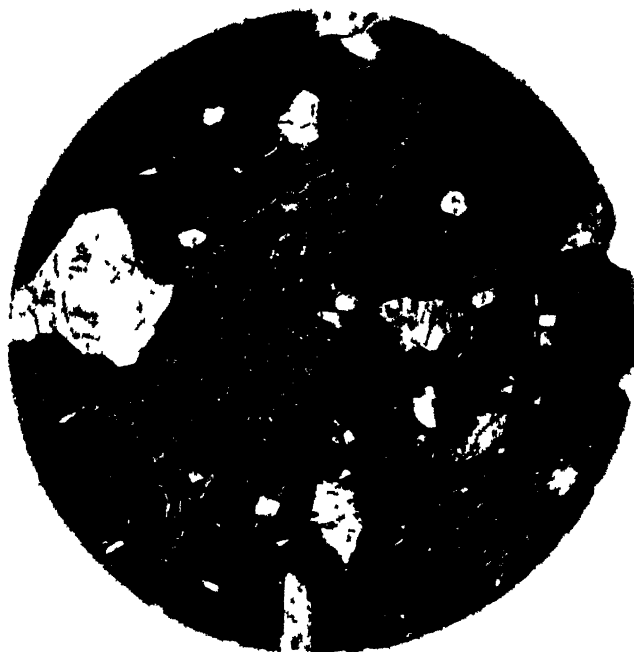


FIG 22.—Specimen C-11. *Enterolithic obsidian*

Plain light. Magnification $\times 30$. Taken to show the fragments of cooled crust intermingled in the rock.

fine-textured basalts. Although this rock cannot be traced to the obsidian in the field, it seems highly probable that it represents the upper part of the obsidian flow.

RHYOLITIC TUFF

The most extensive and prominent accumulations of pyroclastic material are those which cap the Continental Divide from Mount Richthofen

northeast to within three-fourths of a mile south of Lulu Mountain. Along this ridge the tuffs represent the last recorded event in the series of extrusive Tertiary volcanics. Although these rocks are well consolidated, they nevertheless disintegrate rapidly in this lofty exposed position. Consequently they have been more deeply dissected than the associated lavas. In the valleys, oversteepened by glacial erosion, the subsequent rapid accumulation of talus debris from the tuffs has already



FIG. 23.—Specimen C-4. Tuff from Continental Divide, near Lulu Mountain

Plain light. Magnification $\times 30$. Note the mixture of lithic fragments, broken crystals and volcanic ash.

modified the characteristic U-shape. Differences in the pyroclastics relate rather to bedding and texture than to composition or origin. Megascopically they are gray and iron-stained rocks, consisting of irregularly distributed fragments which are, nevertheless, thoroughly indurated. By far the most abundant mineral present is orthoclase, which occurs in a diversity of forms; some of the crystals are large (3 mm.) and euhedral, and others equally large show evidence of having suffered

considerable magmatic corrosion. Most of the orthoclase is present as broken fragments. Twinning is uncommon. The feldspar, although everywhere fractured, has not suffered chemical alteration. However, secondary products derived from the finer material have penetrated and filled up the fractures without affecting the composition of the feldspar.

In addition to orthoclase, there is a small amount of albite and much quartz. Lithic fragments, though less conspicuous than the individual crystals, constitute the bulk of the rock, and in these several rock types are represented, although obsidian is by far the most abundant. The material is porphyritic and shows a marked flow structure. Included within it are fragments of different texture around which the flow lines pass in sweeping curves. Apparently the obsidian represents an entrolithic breccia. It is now almost completely devitrified, and is dusted with secondary iron oxides. Other fragments of salic porphyries, but with coarser textures, are also present and there are a few isolated areas of quartzose shales or grits. The finest material is volcanic ash in which are embedded shards and minute angular crystalline fragments. Secondary alteration has completely oxidized the femic silicates, so that the finer grained material is almost opaque. In addition, there are minor amounts of sericite and leucoxene.

This tuff, by its position, attitude, composition and apparent continuation seems to represent in fragmental form the same rock which as a thick and widespread lava flow forms the capping of Lulu Mountain.

PORPHYRY PEAKS RHYOLITE

In the central part of the area, capping Porphyry Peaks, and on mountain tops on either side of Stillwater Creek farther south, there occurs a rhyolite porphyry of entirely different mineralogy, habit and history. It is brownish gray in color, and remarkable for its large glassy feldspar phenocrysts and rapid mechanical disintegration. The texture is moderately fine and it shows an imperfectly developed trachytic structure. The groundmass consists of quartz grains with microlitic laths of alkali feldspar. Both magnetite and red oxides of iron are scattered through the rock. Feldspar phenocrysts are present both as orthoclase and albite. Although the feldspars have not suffered chemical change, they have in most instances been severely stained and fractured. Both euhedral and anhedral forms occur. Perthitic intergrowths are common. It frequently happens that the euhedral phenocrysts are surrounded by a broad selvage, which is in optical orientation with the enclosed perthitic intergrowths. These highly acid selvages are quite dis-

ting from the zoned structure which is common to the feldspars of this rock. The feldspar phenocrysts have a maximum length of 10 mm. In addition to these, there are large biotite crystals which have been almost entirely resorbed and converted to hematite. In most instances, the original material of the mica has been entirely destroyed. Crystals of apatite of an intermediate size are sparingly scattered through the groundmass. Undoubtedly the history of this rock is as follows: large

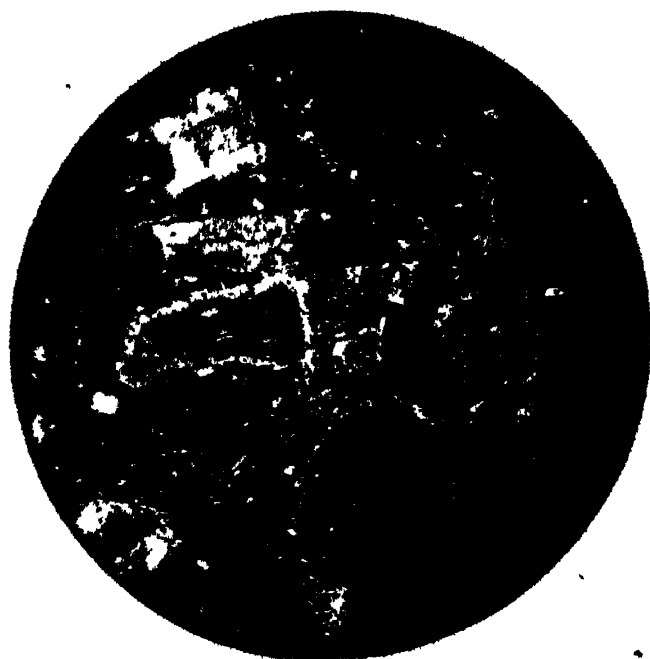


FIG. 24.—Specimen L-15. *Porphyry Peaks rhyolite*

Crossed nicols. Magnification $\times 15$. Taken particularly to show the selvages on the feldspars.

crystals of feldspar and iron-rich biotite were formed under intratelluric conditions; the zoned feldspars attest to rapid crystallization and an equally rapid change in the composition of the melt. This is also shown by the chemical instability of the biotite. The melt was highly charged with mobile end-stage fluids, which produced the perthite and selvages during the final stages of crystallization. The groundmass contains no suggestion of glass, but its variable texture indicates that its solidifica-

tion was rapid though not uniform. The weathered appearance of the rock is due to the setting free of hematite by resorption processes rather than to subsequent changes produced by atmospheric attack.

MICROSPHERULITIC OBSIDIAN

The lava cap of the northwestern mountain in section 10, T. 3 N., R. 76 W., consists of a spherulitic rhyolite flow. This rock is somewhat unusual, both for its structure and mineral composition. The lava shows distinct megascopic flow lines on the lower part, whereas this structure is extremely obscure in the upper part of the flow. Lathophysæ are common throughout the rock, but increase in size upward. Microscopically the rock is seen to consist almost entirely of closely packed spherulites. Some of these are almost round, but in most instances their tendency toward a circular form has been checked by the interference of adjacent spherulites. The average diameter of the spherulites is .2 mm. In the lower part of the lava the arrangement of the spherulites has been controlled by the flowage, so that they are aligned as orderly rows of spherulites of uniform size, parallel to the flowage. The flow lines are straight and parallel except for the curves formed in swinging around an occasional phenocryst. The spherulites are formed of dense clusters of quartz and feldspar, which radiate outward from the center and which are the products of crystallization from glass. Under crossed nicols this radiate structure produces the effect of a uniaxial cross that remains fixed during the rotation of the section. However, the dark bars forming these crosses are not in all cases parallel to the vibration planes of the nicols, but are inclined to them at a low angle. The significance of this is that in some of the spherulites the predominant mineral is feldspar rather than quartz. The extinction angles measured on microlites indicate that this feldspar is acid oligoclase. The flow structure has not interfered with the internal structure of the spherulites, since the lath-like minerals cut directly across the flow lines. This indicates that all movement of the lava had ceased before crystallization began, a fact which is also apparent in the complete lack of deformation in the spherulites. Crystals of intratelluric origin are present as occasional phenocrysts of albite, which are resorbed and fractured. Such crystals are roughly aligned with the flowage. The largest is .8 mm. long. The only other phenocrysts present in the sections examined are small resorbed biotite crystals and an irregular mass of hematite, which is probably secondary. There are also a few minute xenoliths of a basaltic rock, which have been greatly modified.

The lithophysæ are of particular interest, for they have been lined

with and partly filled by high temperature silica minerals. Tridymite, the more common of these, occurs in wedge-like twins and as irregular masses, not only incrusting the surfaces of the gas cavities, but also as an interstitial filling between spherulites. Occasionally the lithophysæ contain cristobalite, but more often a mixture of tridymite and cristobalite. The cristobalite is completely isotropic. The silica minerals owe their origin to the trapping of mineralizers in the gas cavities with the subsequent formation of high temperature minerals,



FIG. 25.—Specimen L-2.5. *Spherulitic rhyolite*

Upper plate plain light, lower plate under crossed nicols. Magnification $\times 30$. Taken to show the spherulitic structure. The interstitial material is largely tridymite.

partly at the expense of material already consolidated: Atmospheric attack has had little effect except where it has been concentrated along the flow lines, producing a slight development of ferric oxide and sericite.

An extensive series of rhyolite flows form the mountain to the east of Mount Richthofen and southeast of Lulu Pass. Although these flows

show slight variations, they are almost identical in mineralogy and form. In color they are white or light gray and all are porphyritic. The groundmass is very fine grained, but nevertheless holocrystalline. It consists of quartz, alkali feldspar, chlorite and sericite. These minute crystals are rather uniform and have an average diameter of about .03 mm. Although under plain light they seem to be uniformly distributed, they are actually grouped in irregular patches as aggregates. This

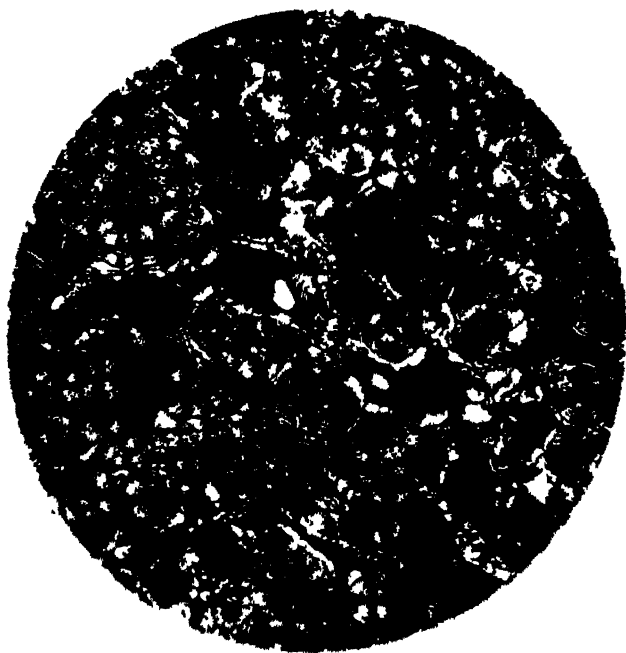


FIG. 26.—Specimen L-2.5. *Spherulitic rhyolite*

patchy arrangement of similarly oriented crystals has probably been produced in an attempt toward differentiation, which has been interrupted by the freezing of the magma. The phenocrysts consist of quartz and orthoclase with smaller amounts of albite and partially resorbed biotite. They show the effect of magmatic corrosion, and the feldspar has been fractured and strained. The rock shows no secondary chemical alteration. This rhyolite is the basal member of the volcanic series at this place.

VOLCANIC ASH

In the western and southern parts of the area the Tertiary volcanic series begins with a salic ash of a somewhat variable composition. On account of the friability of their material the tuffs are only exposed where they are protected by lava cappings or where they have been but recently exposed by erosion. Outcrops of this material occur south-

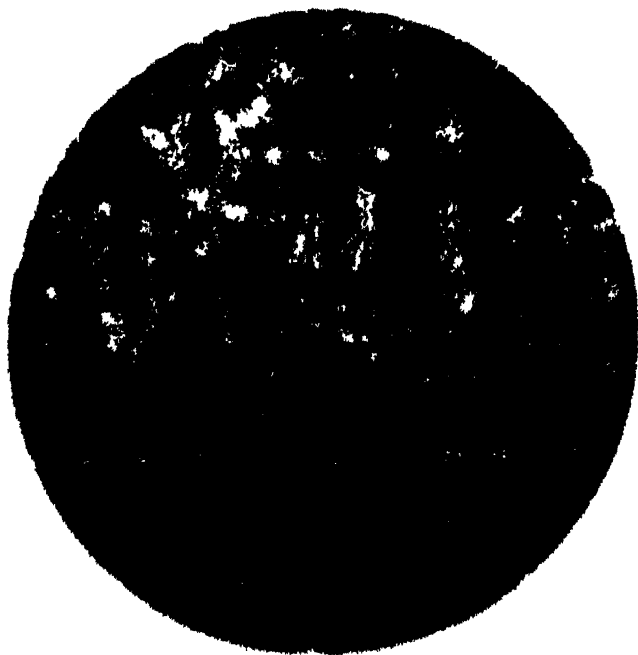


FIG. 27.—Specimen L-2 *Spherulitic obsidian*

Crossed nicols. Magnification $\times 55$. Taken to show the flow lines and spherulitic structure.

east of Trail Mountain section 36, T. 3 N., R. 77 W., and at the southern end of Table Mountain in T. 2 N., R. 76 W. The material is extremely fine textured, white and friable. Occasionally it shows a thin laminated bedded structure, more often it is massive. The bedding, where present, is of lacustrine origin. On Table Mountain the ash beds are intercalated with thin partings of stream-worn conglomerate.

Although the deposition of the lake-bed ash belongs to the early rather than the later Tertiary history, there is no necessity for separating them

in this report from the later and more extensive Tertiary igneous rocks. The ash is made up of particles of two distinct sizes. The larger fragments consist of sharply angular shards showing a variety of composition. With the shards there are mineral grains consisting for the most part of quartz and acid feldspar. In the material from Table Mountain there is, in addition, a large amount of biotite which has been altered to chlorite. It is present as small elongate crystals

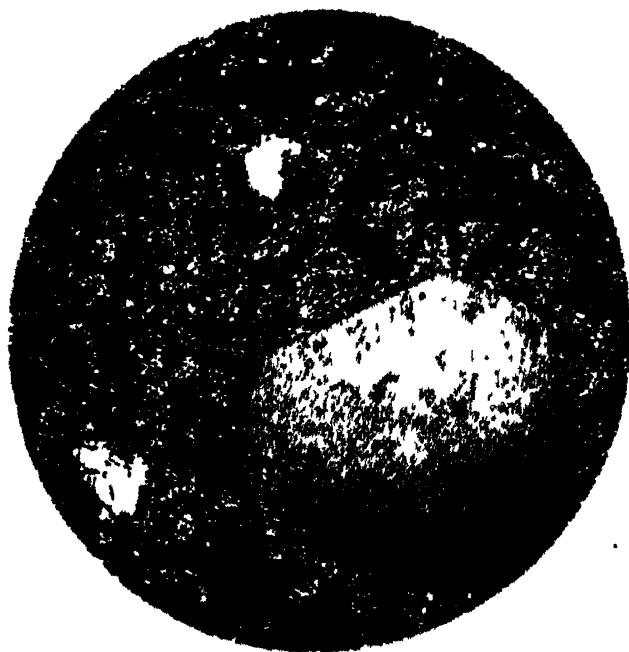


FIG. 25.—*Specimen U 18 Rhyolite*

Crossed nicols Magnification $\times 30$. Taken to show the aggregate forms in the groundmass and the resorption of the phenocrysts

which lie horizontally. The ash from Table Mountain also differs from the material to the west in that the mineral fragments are larger; grains .1 mm. in diameter are common and the fragments rather than the fine ashy matrix form the greater part of the rock. Evidently some disturbance took place after deposition, as is shown by the presence of formless masses of solidified material of finer texture, irregularly distributed so that the bedding in nearby masses of this fine material is inclined.

Although this rock appears white in the hand specimen, the microscope reveals considerable alteration to iron oxides in the fine-grained matrix.

ROCKS OF INTERMEDIATE AND FEMIC COMPOSITION

In contrast with the salic flows and tuffs described in the preceding paragraphs there is also a series of less acid lavas, which range in composition from andesite to basalt. Although these do not show so many structural and type variations as the rhyolites, they are widely distrib-

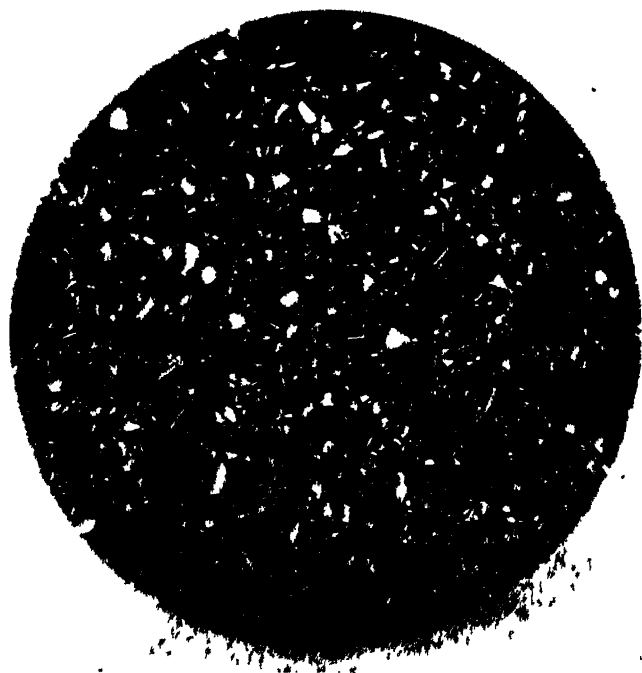


FIG 29.—*Specimen J-19. Volcanic ash from Trail Mountain*

Plain light. Magnification $\times 30$. Note the sharply angular mineral fragments and extremely fine ashy matrix.

uted and form the surface rock over much of the northeast and southeast parts of the region.

In the vicinity of Cameron Pass there are several different members of this group, of which the most abundant is a trachyandesite. The latter consists of several flows with a maximum aggregate thickness of about 800 feet. It extends eastward from Joe Wright Creek to the western scarp of Lulu Mountain, where it is covered by the pink rhyolite

which caps that mesa. The attitude of these lavas is nearly horizontal and, although they have been somewhat dissected by erosion, they nevertheless are characterized by the comparatively level area in the vicinity of Zimmerman Lake. The joints in the lavas are closely spaced, consequently mechanical disintegration takes place so rapidly that the contact with the crystallines below is everywhere covered by talus. The andesite is dense and dark-colored. It contains small, sparsely scattered phenocrysts which show a roughly parallel arrangement as a result of flowage. The most prominent structural feature is the trachytic arrangement of feldspar laths, which are of oligoclase and are twinned after the albite law. They have an average length of .25 mm. and comprise about one-fourth of the rock. The groundmass is extremely fine. It consists of small magnetite grains, shreds of biotite and sericite embedded in a still finer matrix of partly devitrified glass. This matrix is stained and obscured by ferric oxides, formed as a result of surface weathering. The earliest generation of minerals is represented by phenocrysts of untwinned oligoclase and badly resorbed biotite. The feldspars show a strong concentric zoning. Their maximum diameter is 2 mm. In addition to the above normal minerals, there also appears a smaller amount of an isotropic substance which closely resembles opaline silica. This material is found lining and filling cavities in the rock. Frequently these cavities show definite mineral outlines. It is probable that they were formed by the destruction of some pre-existing mineral under the attack of imprisoned gases, and subsequently filled with silica, precipitated by these same gases. The feldspars are remarkably fresh. The only supergene alteration shown is that already noted in the oxidation of the groundmass.

In section 1, T. 7 N., R. 76 W., south of the lavas just described, there outcrops a somewhat different member of this series, a slightly porphyritic oligoclase basalt. This lava is not widely distributed, furthermore it is badly broken up by jointing, so that it shows neither prominent outcrops nor definite physiographic expression. The groundmass is holocrystalline and consists of minerals of more uniform size. It is composed largely of plagioclase laths and microlites, arranged in a closely packed trachytic structure, but without prominent flow-parallelism. This gives a false appearance of diabasic structure. The laths are smaller than in the trachyandesites and comprise nearly all the rock. With the oligoclase there is in the groundmass a large amount of hematite grains, biotite shreds and iron-stained alteration products, including sericite, carbonate, chlorite and limonite. The phenocrysts cover a wide range, but are in no instance more than 2 mm. in diam-

eter. They include oligoclase, titanaugite and hematite masses, which are probably of secondary origin. All the phenocrysts show the effects of igneous attack, partly as a result of resorption, partly in consequence of contained gases. Thus the feldspars are surrounded by selvages of different composition which are rich in inclusions of hematite, whereas the interior of the feldspars is fresh. Similar attack has partly sericitized the feldspar laths of the groundmass. The titanaugite has not

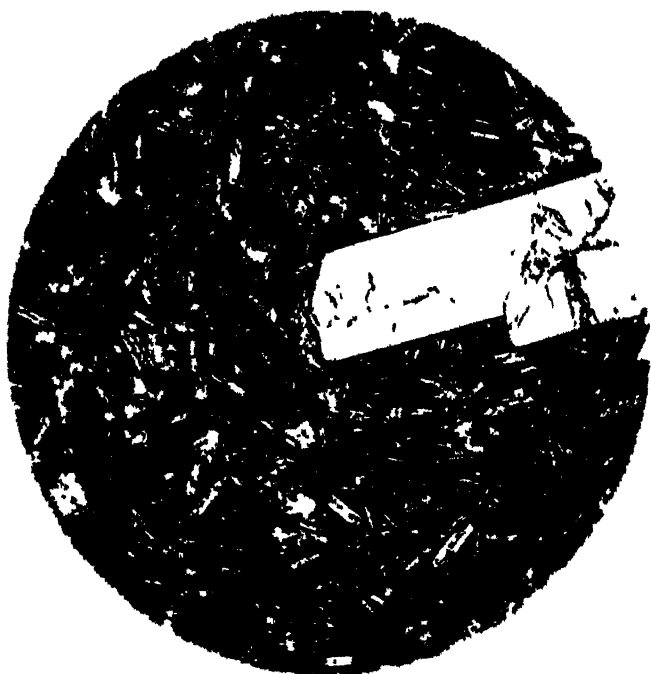


FIG. 30.—*Specimen F-10. Trachyaugite from Zimmerman Lake*

Plain light. Magnification $\times 30$. Taken to show trachytic structure of the groundmass. The obscurity of the matrix is due to the presence of much finely disseminated iron oxide. The phenocryst is oligoclase.

only been altered about the margins and along the cleavages, but in some individuals has been completely replaced by carbonate. The specimens examined show intense alteration by chemical weathering, so that the rock is stained by hematite and hydrated iron oxides largely derived from the femic minerals of the groundmass which are now completely destroyed.

BASALT

In the eastern half of section 12, T. 6 N., R. 76 W., a dense black basalt has been exposed by the excavation for the Michigan Ditch. This rock shows a few scattered phenocrysts. Apart from these it is massive; there is no suggestion of flowage and the joints are widely spaced. The eastern extension of the lava is buried below the talus of Lulu Mountain. The rock itself rests directly upon the ancient crystallines.

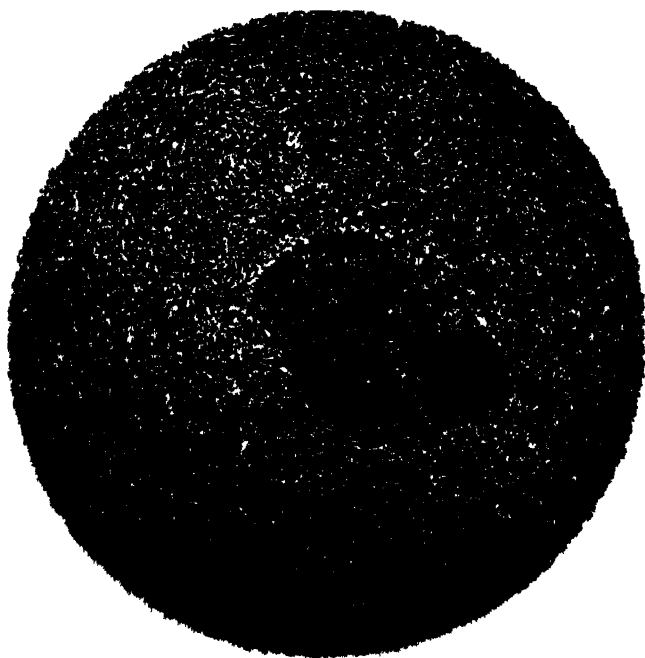


FIG. 31.—Specimen B-20. Basalt exposed on Michigan Ditch

Plain light. Magnification $\times 30$. Taken to show resorbed fassaite phenocryst and finely diabasic structure.

Unlike the trachyandesites the groundmass is holocrystalline and its minerals approximately of the same size. The structure is finely diabasic. In the groundmass feldspar is present both as labradorite and more sodic varieties in microlitic laths. With the feldspar in the groundmass there are small crystals of almost colorless augite, grains of magnetite and an unusually large amount of epidote in small irregular crystals. Leucoxene, carbonate, sericite and serpentine are present as

alteration products. Fassaite is present as phenocrysts, but is not abundant. Although this mineral has not suffered chemical alteration, it has been so resorbed that the margins present bold sweeping curves, interrupted by deep re-entrants. The presence of other ferromagnesian phenocrysts, now destroyed, is suggested by large irregular patches of shredded biotite. Untwinned plagioclase of a highly calcic composition forms the largest crystals. These are cut by fractures subsequently filled by a sericite carbonate mixture; otherwise they are unaltered. There has been a slight replacement of feldspar by introduced pyrite. The mineralization which brought the sulphide was also responsible for the epidote, sericite and carbonate, which replace the normal orthotectic rock minerals. These changes were probably brought about during the consolidation of the lava, since there is nothing to indicate a subsequent igneous attack from a foreign source.

TRACHYANDESITE SERIES

The most widespread lava in the region is a trachyandesite, which forms the cap rock of the mountains from Apiatan Mountain southward. This rock is remarkable for the variations in its internal structure and texture; variations which result partly from differential cooling, partly in response to the contained gases. The following types are of frequent occurrence:

Massive trachyandesite
Scoriaceous lava
Amygdaloidal lava
Devitrified glass

In addition, there are occasional tuff lenses. All the types above show variations brought about by different degrees of primary flowage. The glassy and scoriaceous members yield readily to weathering and erosion; the more massive layers are resistant and impart a flat mesa-like topography to the mountains which they cover. In the southern part the lava lies directly on the ash previously described; in the north it rests upon the pre-Cambrian rocks.

With the exception of the rapidly chilled lava the material is a dark brownish-gray; frequently it has a reddish tinge produced by the oxidation of the ferromagnesian minerals. The vesicular cavities vary considerably in size. The largest are more than two inches long. They may be present in very small numbers, or they may constitute sixty per cent of the rock. Frequently in the more scoriaceous specimens they show a parallel elongation as a result of flowage. The proportion of

amygdaloidal fillings or linings in the cavities differs from place to place and is independent of locality, horizon or texture of the rock. A given vesicular specimen may be free of amygdules; it may show all the cavities filled, or it may show any gradation between the two extremes. Only the andesite which shows evidence of having flowed with slight viscosity is entirely free from the vesicular structure.

The most persistent characteristic of the rock is its trachytic structure. This, with minor exceptions, is composed of laths of oligoclase-andesine, which in most instances are simply twinned. The size and abundance of the feldspar crystals depend largely on the consolidation history, which is not constant throughout. Where cooling has taken place rapidly, the feldspar is present as microlitic crystals rather than as laths. Feldspar may constitute from twenty to eighty per cent of the rock. Tabular forms and multiple twinning are uncommon. Frequently the laths show a high degree of parallelism as a result of flow—a feature which is particularly common in the non-vesicular andesite. The specimens which contain much feldspar are holocrystalline; others show different amounts of residual glass, of which nearly all is completely devitrified.

In the groundmass there is much granular magnetite, which is mostly the product of resorption of ferromagnesian minerals. That resorption has been an active agent in the history of the rock is shown also by the nature and distribution of the biotite. This mineral is present in large quantities, but never in its normal form. It occurs partly replacing small idiomorphic augite crystals, partly as fine shreds in shapeless aggregates with other minerals of a secondary history, where it has been produced by the alteration of iron-bearing phenocrysts. The biotite is uniformly of a deep brown, iron-rich variety except in isolated cases where it has been converted to chlorite. Phenocrysts are not common; however, there is an occasional euhedral crystal of alkali feldspar, usually albite or microcline. One specimen contains augite phenocrysts surrounded by heavy reaction rims of serpentinous matter. The alteration products consist chiefly of carbonates with some hematite, sericite and leucoxene. Weathering has had only a slight effect, and this upon the groundmass where it is present. The feldspars are fresh.

In contrast with the definite trachytic material described above, there is also much glassy material in the upper part of the lava. The glass tends to be massive; it seldom contains gas cavities although flow banding is common. Megascopically it resembles opaline silica in form and conchoidal fracture. It commonly shows either a bright ochre or deep scarlet color, as a result of the finely disseminated particles of ferric

oxide. The glass seldom occurs in place. The contact between the glassy material and the normal trachyandesite is rather sharp, and is usually marked by an abundance of wide horizontal cavities filled by microcrystalline silica minerals. These cavities appear fusiform in vertical section and were formed by the pressure of rising gases, which were dammed up upon encountering the already solidified glassy crust of the lava.



FIG. 32.—Specimen J-13-C. Trachyandesite from Trail Mountain
Plain light. Magnification $\times 60$. Taken to show the trachytic structure.

The glass which has not been devitrified possesses a strong banded structure and a low refringence, both of which are more suggestive of obsidian than of andesitic glass. Devitrification has been complete in nearly all material; generally it has given rise to irregular aggregates of interlocked minerals, although certain areas show a tendency toward spherulitic arrangement. There has been a slight development of tridymite in the gas cavities. The minerals developed by devitrification are

quartz, feldspar and iron oxides, which show different degrees of hydration.

The amygdules have been formed as a series of encrustations on the walls of the vesicular cavities. Hence they show a strong concentric structure, which has been produced not only by successive layers of different minerals, but by a change in mineral structure in response to changing environment. The amygdules are frequently hollow and are lined with well-developed crystals. The minerals are restricted to calcite

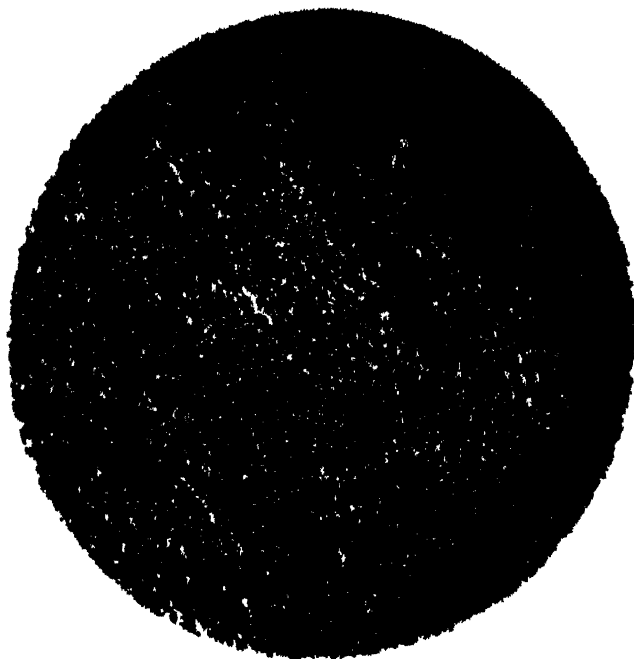


FIG. 33.—Specimen L-18. *Trachyandesite from Stillwater Creek*

Plain light. Magnification $\times 30$. Taken to show the prominent flow structure recorded in the attitude of the feldspar laths.

and various forms of silica. In most instances the calcite has been the first substance precipitated and so forms the outer ring. Following the calcite there frequently appears a layer of radiating fibrous quartz or chalcedony, which is followed by an inner layer of normal quartz crystals with well-developed faces. Commonly the cavities possess a lining of tridymite. Tridymite occasionally alternates with chalcedony layers.

INTRUSIVE ROCKS

At two localities the Tertiary igneous series is represented by intrusive rocks. Dikes of quartz monzonite porphyry outcrop on either side of Willow Pass on the Continental Divide. In the vicinity of Lake Agnes there are several irregular bodies of salic porphyry, as well as a granodiorite of abyssal habit. The outcrops of the granodiorite are grouped about Lake Agnes as inliers of the subjacent mass.

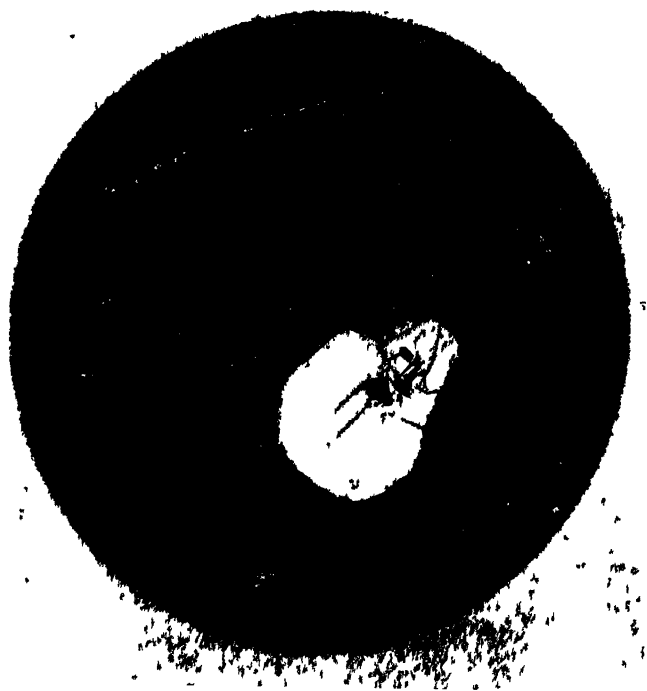


FIG. 34.—Specimen L-21-a. Andesite obsidian from Stillwater Creek

Plain light. Magnification $\times 30$. This is a glassy phase of the andesite illustrated in the two preceding photomicrographs. Note the crystallization which has taken place along the flow lines

QUARTZ MONZONITE PORPHYRY

On Parkview and Radial mountains, in the extreme western corner of the region mapped, there are several strikingly persistent quartz monzonite porphyry dikes. These cut vertically through the Denver arkose. On account of their greater resistance to erosion they stand out prominently, and may be traced for several miles, as vertical walls, pur-

suing a straight or slightly curved course across country. The dikes are from thirty to sixty feet wide, and occasionally form ridges more than a hundred feet high. Radial Mountain itself is formed of these dikes converging at its summit, whence its name. The prominent ridges and converging spurs which form the eastern end of Parkview Mountain owe their topographic sharpness to the presence of the dikes. The appearance of the quartz monzonite porphyry is striking and unusual on ac-



FIG. 35.—Specimen K-7-B. Amygdule from Table Mountain

Crossed nicols. Magnification $\times 60$. Taken to show the successive layers in the wall of the amygdule. Note the outer layer of calcite, followed by chalcedony and quartz.

count of the large and almost perfect orthoclase phenocrysts. These are frequently over an inch in length and often occur as Carlsbad twins. The feldspars retain their form after the remainder of the rock is weathered and may be picked out of the residual soil adjacent to the dikes. In addition to the orthoclase there are phenocrysts of albite and occasional crystals of quartz. A prominent feature of the feldspar phenocrysts is the strong modification of the margins and along the

cleavages. This attack of igneous origin has produced an aggregate of chlorite, sericite and carbonate, which stands in such sharp contrast with the body of the phenocrysts that it is easily discernible in the hand specimen. Certain phases of the rock contain biotite, altered titanite, and magnetite also as phenocrysts. The groundmass is holocrystalline and is fine grained. Its most abundant constituent is an intermediate plagioclase, which is present as small untwinned crystals. This feldspar



FIG. 36.—*Specimen X. Amygdaloidal filling. Table Mountain*

Crossed nicols. Magnification $\times 30$. Taken to show successive layers of chalcedony.

is closely interlocked with the other groundmass minerals, chiefly chlorite, ilmenite, apatite and alteration products. The rock shows the effects of both weathering and hypogene alteration. The secondary minerals are carbonate, which to a great extent replaces the feldspar and biotite, and also serpentine and chlorite produced in part from the biotite, in part from completely destroyed ferromagnesian minerals. Leucoxene is present throughout the rock as a result of the decomposition of the titanium-bearing feric minerals. This quartz monzonite

porphyry has been very briefly described by Zirkel (23, pp. 68-70), and its presence also noted by Beekly (3, p. 80), Marvine (20, p. 174), and King (13, p. 122).

The consolidation history is somewhat complex and is illustrated by the changes which apparently took place before the mass became completely solid. It would seem, in the first place, that the earliest formed materials were not in equilibrium with the melt, as is shown by the re-



FIG. 37.—*Specimen H-1. Quartz monzonite porphyry or dellenite from Willow Pass*
Plain light. Magnification $\times 15$. Taken to show altered orthoclase phenocrysts.
Note aggregate structure of the groundmass.

sorption and extensive reorganization of the phenocrysts. Highly differential rates of cooling are evident in the variability of the texture and even the mineralogy of the groundmass within short distances. Superimposed on these changes and variations are the effects which were produced by the end-stage juices. This attack was responsible for the breaking down of the titanium-bearing minerals to leucoxene, for the formation of the disseminated sericite, chlorite and carbonate, which

are so abundant throughout the groundmass, and for the marked but localized attack upon the feldspars.

GRANODIORITE

The granodiorite, which is intruded in the vicinity of Lake Agnes, is the only member of the Tertiary igneous series that possesses an abyssal habit. The distribution of its outcrops is somewhat patchy. The largest exposure occurs south and southeast of Lake Agnes. In each

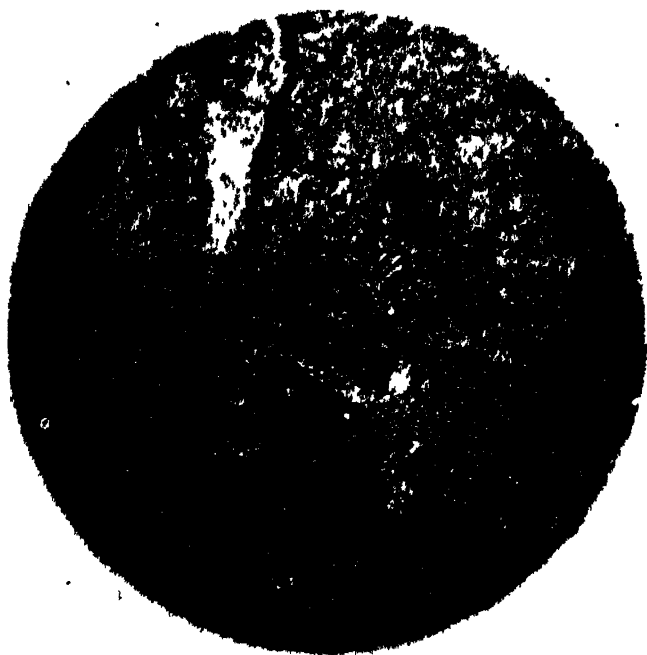


FIG. 38—*Specimen D-9. Granodiorite, south of Cameron Pass*

Plain light. Magnification $\times 30$. Taken particularly to show micrographic intergrowth of quartz and feldspar. Most of the gray material is chlorite.

instance the igneous contact is hidden from view by either talus or vegetation. This intrusion is older than the extrusive rocks of the immediate vicinity, and belongs to an earlier stage of Tertiary vulcanism. This is apparent from the fact that the tuff which caps the Continental Divide in this region rests directly upon the eroded surface of the grandiorite. In the hand specimen the rock has a speckled appearance, which results

from the sharp contrast between the unusually white feldspar and the green femic minerals. Under the microscope it shows the massive interlocked structure common to granitoid rocks. Its salic constituents are quartz, orthoclase feldspar, albite and albite oligoclase. The feldspars are somewhat lath-like in form and are so arranged as to produce a rough pseudo-ophitic structure. Carlsbad twins and prominent zone structures are common. The feldspar has suffered from deuteric attack.



FIG. 39.—Specimen F-29. *Syenite porphyry from Lake Agnes*

Plain light. Magnification $\times 30$. Note the fractures in the feldspars filled with limonite.

This attack is exhibited not only by the formation of a great deal of sericite, saussurite and related products, but also by the microperthitic intergrowths in the feldspar. Although most of the quartz is present as normal crystals, much occurs in a micrographic intergrowth with the more acid feldspar—a feature also brought about by the deuteric attack. The primary femic constituent of the rock is a pale brownish-green hornblende with lesser amounts of biotite. Little of these two minerals

now remains. They have been largely altered by resorption to chlorite, serpentine and magnetite. The hornblende and its products are distributed in patches through the rock. The grandiorite weathers rapidly, consequently no fresh material can be obtained from its outcrops. For this reason the specimen here described shows the effects of weathering in addition to the hypogene deuteric alteration.

SYENITE PORPHYRY

In the complex structure about Lake Agnes in the north end of the area, the downfaulted beds of Cretaceous grits have been intruded by irregular bodies of hypabyssal salic rocks. The rock briefly described below is typically representative of these porphyries.

In this material the groundmass is holocrystalline, dense and somewhat micrographic. Its essential constituents are oligoclase and alteration products of both primary and secondary origin. Although this is related chemically to the trachytes, there is no suggestion of flowage. The most abundant phenocrysts are highly sodic feldspars, strongly idiomorphic and decidedly inequidimensional. They show Carlsbad and simple albite twinning. Biotite of a deep brown variety constitutes the other phenocrysts. This, itself, has been partly resorbed to form magnetite and chlorite, and owes its origin to the breaking down of a blue-green soda-rich hornblende. Magnetite produced by resorption is freely scattered as grains and irregular patches through the rock. The rock shows considerable deformation history; notably in the broken feldspars which have been pulled apart, and in the abundant fracture systems and strain shadows of the phenocrysts. Frequently the feldspars have been broken, separated, offset, and the intervening space filled up by groundmass material. Supergene alteration of the ferromagnesian minerals has discolored the rock with an intimately penetrating limonitic stain. This material is particularly noticeable in the fractures of the phenocrysts, where it has followed the breaks in an extremely penetrating manner. It is perhaps best classified as a soda-rich syenite porphyry.

IGNEOUS ROCKS OF UNCERTAIN AGE

GRANITE PORPHYRY

In the northeastern part of T. 5 N., R. 76 W., forming the bulk of Red Mountain and the spurs immediately north, there is a coarse pink granite porphyry of a hypabyssal habit of which the age and structural relations are uncertain. In consequence of the glacial oversteepening and the rapid mechanical disintegration of this rock its contacts with the

country rock are everywhere buried below talus or moraine deposits, so that it is not possible to determine whether it is one of the ancient intrusives or whether it belongs with the Tertiary volcanics. The texture is moderately fine though highly variable, and there is every gradation in the size of the crystals of the groundmass and the phenocrysts. Its structure is holocrystalline, massive and irregularly granitoid. The crystals are closely interlocked, but possess a rough equidimensional

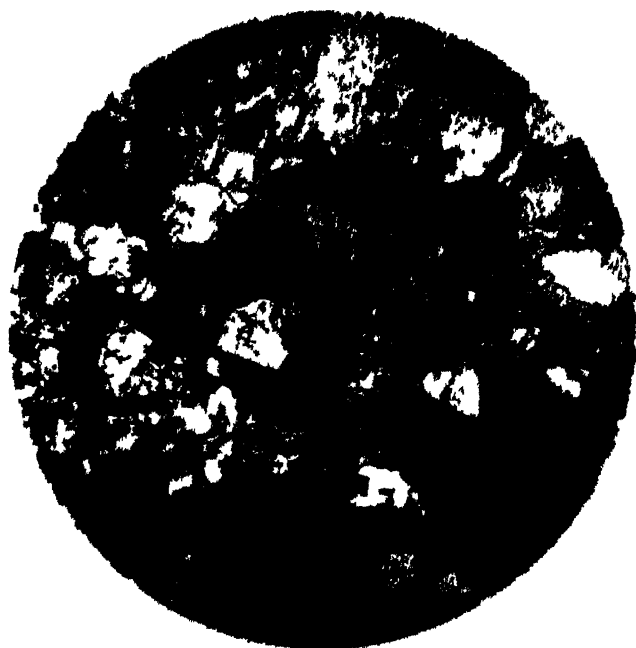


FIG 40.—*Specimen M-10. Granite porphyry from Red Mountain*

Crossed nicols. Magnification $\times 30$. Taken to show the irregularity of texture and the perthitic intergrowth. Note also the crenulate margins and lack of femic constituents.

habit, which may be described as granular. Quartz, orthoclase, albite, muscovite and biotite are present in the groundmass. There is also a small amount of disseminated chlorite, serpentine and limonitic material. The phenocrysts consist of highly irregular crystals of quartz and orthoclase together with a few scattered crystals of albite, which are intermediate in size between the phenocrysts and the groundmass. The maximum diameter of the phenocrysts is 3.5 mm. All the orthoclase

crystals have been so modified by end-stage igneous activity that they now consist of almost equal parts of potassic and sodic feldspar in perthitic intergrowths. Further attack of the same kind resulted in the "dusting" of the included sodic feldspar by saussurite. The margins of both phenocrysts and groundmass crystals show a highly crenulate form, which can only be attributed to a period of deformation, in which the rock was mildly sheared. The shearing is indicated by the variability of texture and the partial destruction of its original porphyritic habit. As a result of recrystallization, strain shadows and similar stress effects have been obliterated, and only the tendency toward a granular structure remains as evidence of the deformation. The fact that none of the Tertiary igneous rocks of the region shows a similar deformation history is indicative that this intrusive belongs to an earlier period. The rock is somewhat remarkable for the very small amount of ferromagnesian and accessory minerals.

It is as though this intrusive, with its relatively large vertical extent in comparison with its area, were a cupola or offshoot of some larger sub-jacent igneous body. If this is actually the case, its highly salic composition may have been produced as a result of an advanced stage of differentiation in the higher parts of the cooling magma. This hypothesis is in keeping with the presence of so much perthite and the subsequent highly selective attack on the feldspar. The rock in place nowhere shows the effects of chemical weathering, not because of any unusual stability of composition, but rather on account of the vigorous mechanical breaking-down, which is constantly exposing fresh surfaces to the atmosphere.

GEOMORPHOLOGY

In this region of high relief and of dissimilar rock types, the development of the land forms is so intimately related to the structural history that the two could not be treated separately without much repetition. In the further interest of clarity and conciseness the steps which gave rise to the present land forms are here described as far as possible in chronological order. Under the heading of geomorphology are included structural geology as well as geologic and physiographic history.

EVOLUTION OF THE PRESENT STRUCTURE

The earliest recorded event in the history of the region was the extrusion of the basic tuffs and lava flows during Archean time. Before the close of that era, this volcanic series suffered intense dynamic meta-

morphism and intimate magmatic injection, thereby producing the crystalline foliate rocks which form the basement complex of the region. Before the close of pre-Cambrian time the mountains uplifted during the dynamic metamorphism of the ancient rocks were levelled by erosion. Although no remnants of Algonkian rocks are here preserved, this system is represented by 24,000 feet of clastic rocks and limestones in the northern end of the Medicine Bow (4, p. 619). It is probable that the Algonkian rocks once extended over this area and were subsequently removed by erosion. The records of early and middle Paleozoic time are also wanting. It is not possible to ascertain whether this last omission is the result of erosion or of non-deposition.

During the Carboniferous and Triassic time the country now uplifted to form the Colorado Rockies was a site of deposition. Although the sediments then laid down have been stripped from the flanks and summits of the higher mountains, there is no question concerning their former extension over the area. Evidence of their continuation across what is now the Front Range is found in the presence of limestone and the Chugwater formation in the down-faulted blocks of Cameron Pass. The abrupt change in the lithologic character of these two formations indicates the passage from marine to continental environment. The next record is that of the late Cretaceous when there was an encroachment of marine waters, indicated by the somewhat isolated outcrops of fossiliferous shales, both at Cameron Pass and Trail Creek. The gritty composition of the sediments indicates conditions of near-shore deposition.

Before going further with the discussion it is advisable to sum up the geologic conditions prevailing immediately preceding the advent of the Laramide Revolution. At that time the essential elements consisted of a highly disordered body of crystalline rocks, peneplaned and buried beneath sediments. The sediments were alternately of marine and continental origin. In so far as can be ascertained, they were lying undeformed where they were deposited.

The structure briefly outlined above was modified by the complex diastrophism at the close of the Cretaceous. This disturbance, the Laramide Revolution, not only uplifted the whole region but also folded the sedimentary rocks. The preservation of Mesozoic sediments in both North and Middle parks, as contrasted with their removal to the east, indicates strongly that the diastrophism was in many respects similar to the later upward monoclinical elevation of the Front Range. Hence it is probable that the parks west of the Continental Divide received their basin structure at this time. The faulting which preserved the

Paleozoic and Mesozoic strata was a phase of the same disturbance. Although the faulting and the folding may not have been contemporaneous, it is clear that the faulting occurred before the advent of the Tertiary volcanics. The steep dips produced as a result of Laramide folding locally exert a marked control on the present-day topography. Hogback ridges formed by the steeply dipping beds of Pierre sandstone in the valley of Trail Creek are typical examples. The faulting is only evident in the vicinity of Cameron Pass.

Following the diastrophism profound denudation took place, either in latest Cretaceous or early Eocene time. Except where, as previously noted, they were preserved in down-faulted blocks, denudation beveled the folded Mesozoic strata and completely removed them from the northern and eastern parts of the area. Whether the cycle of erosion is that which resulted in the Flat Top peneplane, it is not possible to determine. In the area there are no broad upland levels which may be compared with the surface on Trail Ridge and Flat Top Mountain to the east. Furthermore it is not even certain that erosion passed to that advanced stage of denudation which would produce a peneplane. However, the general region of the Front Range was reduced to a relief low enough to permit the widespread deposition of the water-worked andesitic material which characterizes the base of the Denver formation in Middle Park and the Denver Basin.

The cycle of erosion was brought to a close by rapid uplift or, rather, by a series of rapid interrupted uplifts. The evidence for such diastrophism is seen in the alternation of coarse conglomerates with fine sandstones, separated by sharp non-gradational contacts. Further evidence of the steepening of river gradients is presented in the condition of the mineral grains of the sediments, for they were deposited rapidly before attrition or chemical decay could destroy the less resistant minerals. Thus it may be inferred that the deposition of the strata, the Denver formation, was in part contemporaneous with the uplift. There is no evidence to indicate that the sedimentary beds in the region were peneplaned or, on the other hand, that they were ever basined and covered by later sediments during the formation of the Rocky Mountain peneplane.

The next event of which there is definite evidence was the intrusion and extrusion of the Tertiary volcanic series. The effusive members of the series, the tuffs and lavas, were extruded on a surface of fairly high relief, which is apparent in the lack of accordance shown by the contact of these rocks with the crystallines in the Cameron Pass region. Nowhere in the area is there a suggestion that the igneous rocks were cut

by the Rocky Mountain peneplane. Thus it is highly probable that the volcanic activity took place late in the Tertiary history.

The last step in the structural history was the uplift which gave rise to the present cycle of erosion. This uplift, like the others which preceded it during latest Cretaceous and Tertiary time, consisted of a vertical arching movement. The monoclinial warping so produced elevated the crystalline complex of the Front Range but did not affect the bordering sediments on the eastern side of the range except by curving up their margins around the edges of the uplift. On the western



FIG. 41.—General view of the Front Range looking southeast from the Continental Divide at Lulu Pass

The rocks comprising these mountains are massive crystallines. Notice the bold rounded form of the uplands as contrasted with the concave ice-moulded valleys.

side of the Front Range the uplift of the Rockies was accompanied by the uplift of the parks to their present high altitude. It is also believed that the Divide between North and Middle parks came into existence at the same time.

RECENT PHYSIOGRAPHIC DEVELOPMENT

Before proceeding with the discussion of the recent physiographic history, it is appropriate to state what is known concerning this area in comparison with the physiography of the Front Range to the east and

southeast. On the Front Range two peneplanes are generally recognized (11, pp. 21-84), (17, pp. 1-19) and (19, pp. 495-512). The earlier of these, designated the Flat Top peneplane, stands with its monadnocks along the crest of the Continental Divide at an altitude in excess of 11,000 feet. The later, Rocky Mountain peneplane, is best displayed to the east of the Divide. Both of these peneplanes were developed upon resistant crystalline rocks whose structures they bevel. Little is known concerning the subsequent deformation of the Flat Top peneplane. However, restoration of the Rocky Mountain peneplane surface shows that the latter was elevated by an irregular vertical movement. Its present form is that of a broadly curved arch of which the eastern slope is surprisingly gentle. The location of the Continental Divide with its remnants of the Flat Top peneplane close to the western margin of the crystalline rocks, which form the Front Range, indicates strongly that the uplift of the Rocky Mountain peneplane was highly asymmetrical. As a result of the steepening of the river gradients on the "Western Slope," erosion has succeeded in destroying the uplifted peneplane on the western side of the Continental Divide. A second cause of the non-preservation of the peneplane may be attributed to the erosion of the rocks of Middle Park. For the most part they consist of sandstones and non-resistant lavas, which in contrast with the crystallines of the Front Range are readily eroded. The uplift of the Rocky Mountain peneplane is in all probability the same movement which raised the divide now separating North from Middle Park and thereby imparted the steep dips to the Denver formation.

The present topography is the product of fluvial and glacial erosion, working on both simple and complex structures involving resistant and non-resistant rocks. The uplift which commenced the present cycle gave rise to vigorous stream erosion and later among the higher mountains to Alpine glaciation that has but recently ceased. There is evidence of only one period of glaciation. The master streams, later modified by glaciation, owe their origin partly to the nature of the initial uplift, partly to differences in rock resistance. Thus the upper south-flowing part of the Colorado River is subsequent and follows the cleavage of the crystalline rocks. On the other hand, Willow Creek and the Michigan are consequent on the uplift.

The present cycle of erosion is generally referred to as the Canyon Cycle (17) by virtue of the deep dissection of the upland by fluvial and glacial erosion.



FIG. 42.—*Nokhu Crags*

Note the sharp arête in the background. The horizontal white line is the Michigan Ditch, which diverts the drainage to the east side of the Medicine Bow Range.



FIG. 43.—*Moraine in the cirque east of Nokhu Crags*

Shows steep moraine front and the large angular blocks. Compare this with the preceding photograph.

GLACIAL GEOLOGY

Here the most conspicuous features of earth sculpture are those resulting from glacial erosion. Intense Alpine glaciation has produced a large number of cirques and over-steepened valleys among the higher mountains in the immediate vicinity of the Continental Divide. The topographic sharpness of the Divide is further accentuated by the arêtes and horns. Although more than one epoch (1, pp. 385-409) and (15, pp. 502-529) of Pleistocene glaciation has been recognized in several mountainous regions of Colorado, here there is evidence of but one, the latest stage. If earlier glaciation activity took place here, as is highly probable, its effects have been totally obscured by Wisconsin glaciation.

The cirques are most prominently displayed on the east side of the Never Summer Mountains. They have also been developed to the north of the Continental Divide in the vicinity of Lake Agnes and Nokhu Craggs. In the extreme western portion of the area, three large cirques have been carved from the southeast face of Parkview Mountain. These are isolated from the others, just as Parkview Mountain is isolated from the other lofty peaks. It is worthy of notice that nearly all the cirques face in an easterly direction. Apparently there is no relation between the size of the cirques and rock resistance; those which have been carved from the massive indurated crystallines are just as large as those whose walls consist of friable sandstone. It is true, however, that the sharp divides between the cirques on Parkview Mountain consist of massive porphyry dikes. Many of the cirques are marked by deep rock basins several of which contain lakes. Lake Agnes and the chain of lakes immediately east of it are the best examples. In the smaller cirques the original sharpness of the walls, as well as the moraine, has been largely obscured by talus sheets. The larger cirques, on the other hand, contain typical moraines characterized by coarseness of the material composing them and by steep fronts. On several of the moraines vegetation has as yet been unable to obtain a foothold. Protected by the shadows of the steep slopes, snow banks linger throughout the year, the remnants of a slowly dying glacial epoch.

Typical U-shaped troughs have been developed by the change from fluvial to glacial erosion. Although this effect of glaciation is of common occurrence in the area, it is especially well displayed by the over-deepening and oversteepening of the northern part of the Colorado River. Here there is a drop of 1,000 feet from the shoulder marking the intersection of fluvial and glacial profiles, down to the present stream level. Similarly, the courses of the major streams, north of the



FIG. 44.—*Rock-basin lake north of Mount Rukthofen*

The notch in the middle distance has been cut through both moraine and bedrock. It forms the outlet to a chain of three rock-basin lakes.

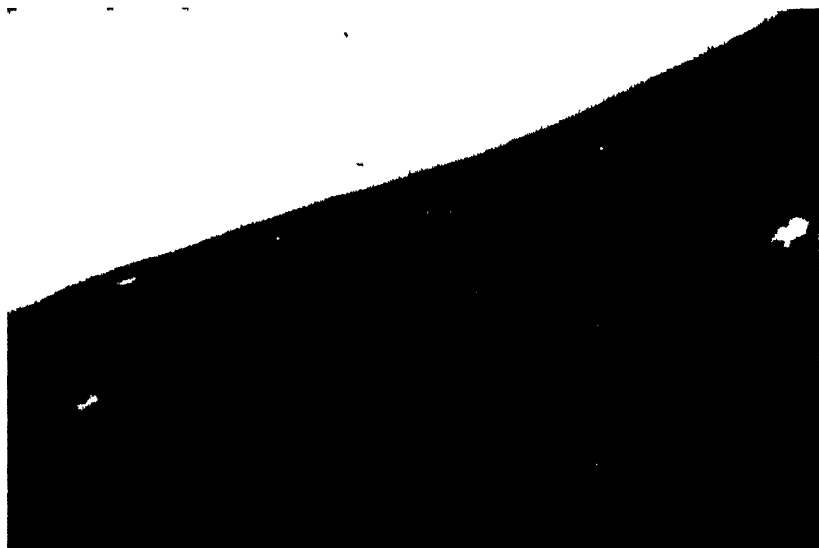


FIG. 45.—*Western cirque on Parkview Mountain*

The rock in the background is arkose. Note that the distant slope of the mountain is nearly a dip slope.

Continental Divide, notably Michigan and Joe Wright Creeks, have been deepened by glacial erosion and show the same type of compound profile, although the catenary curves of the profiles have been modified by talus from the rapidly disintegrating volcanic rocks. The glacial overdeepening of the valleys has necessarily resulted also in the development of many truncated spurs. The most typical occur along the east side of the upper part of the Colorado River. They are splendidly displayed on the topographic map by the blunting of the contours on the east sides of the mountains. Along the northern part of its course the Colorado is fed by mountain streams which, after draining the cirques, plunge to the master stream below in a series of short steep cataracts. Hence, each is a hanging cirque tributary to the Colorado River.

In the valleys of Michigan Creek and the Colorado River moraines are prominent, but are not developed in an amount such as one would expect from the erosion which has taken place. This is due in part to their reworking and modification by fluvial agencies and in part to their concealment beneath river deposits. Ground and terminal moraines can both be recognized, but recessional moraines are most conspicuous. In section 9, T. 6 N., R. 76 W., Michigan Creek flows through an irregular and confused accumulation of glacial debris. Its valley is marked by a steep knobby topography studded with undrained lakes and marshy depressions. Farther upstream the valley floor is occupied only by fluvial deposits. The valley moraines of the Colorado River occur in greatest profusion in the vicinity of Grand Lake, where there is a series of crescentic recessional moraines, convex downstream. The abundance of till in this vicinity has been ascribed to the presence of glaciers converging at this point from the valleys to the east of Grand Lake (20, pp. 154-192). The topography is rough, characterized by undrained hollows. The boulders of the till are chiefly of coarse-textured gneiss and granite, consequently they seldom preserve glacial striae, although faceted faces are not uncommon. The larger moraines in the Colorado valley have been piled up about roches moutonnées forms. Although the latter are well-rounded, none of them display polished surfaces.

RIVERS AND DRAINAGE

The control exerted by rock structure and resistance is more marked in the areas of sedimentary and effusive rocks than in the crystallines, for the latter occupy the higher altitudes where most of the streams follow glacial troughs. Where the streams are cutting down through horizontal sandstones or lava flows, the valleys are steep, narrow and canyon-like, with walls vertical in places, a conspicuous feature of Willow and

Stillwater creeks. The more open valleys of the tributaries and the headwaters of Willow Creek are in striking contrast.

A brief examination of the map shows that the valleys last named possess a strikingly sub-parallel arrangement. In the northeastern part of the Willow Creek basin the streams flow southwest, in the center they flow west, and farther south their course is southwest. In each case the direction of the stream course is parallel to the strike of the Denver arkose. Here the adjustment of streams to structure is almost complete. Each of the subsequent tributaries follows the outcrop of a less resistant layer, whereas the divides are formed of the quartzitic strata and conglomerate. The migration of the streams down the dip has resulted in a marked asymmetry of valley profile. In such instances the steeper valley wall is on the down-dip side. Such lack of symmetry, however, is not apparent where the dips are in excess of 40° . The tributaries of Willow Creek, immediately south of the Continental Divide, and the secondary tributaries farther south enter the main stream at right angles. In other words, they are resequent in origin and follow the dips and not the strikes. Since the subsequent tributaries of Willow Creek follow the weaker beds, they have reached a later stage of development than Willow Creek itself or Stillwater. Thus the tributaries are now in late youth and early maturity, whereas the main streams are still characterized by rapids and waterfalls. The profile of Willow Creek is made irregular by the presence of several local base-levels controlled by resistant rock material standing at a high angle. In the northern part of Willow Creek erosion has been held in check by the quartz monzonite dikes. Farther south erosion is limited by the tough igneous material at the base of the Denver. The presence of temporary base-levels has given rise to lateral planation immediately above them. Such planation has been followed by the deposition of narrow flood plains of rich alluvial soil. On them are located the meadows which support a small but thriving cattle industry. The river follows a meandering course across the flood plains, and the meanders are susceptible to sudden shifting in time of flood. Consequently the preservation of the meadows necessitates much work on the part of the ranchers in keeping the stream to its channel. In addition to the flood plains, the river deposits have been augmented by the alluvial fans. At the mouth of Gold Run an alluvial fan was deposited which was of sufficient size to force the channel of Willow Creek to the opposite side of the valley. During the closing decades of the past century the fan was the site of gold placer operations. The alluvial fans, accumulated by the tributaries in the vigor of their youth, are now being dissected.

In the upper part of its course the Colorado River flows across a flood plain for several miles. The origin of the flood plain is somewhat complex, and in the strictest sense of the term it is perhaps not actually a flood plain. With the exception of the features mentioned below, its surface is level. The upper material consists of fluvial sands, muds and fine gravel. Below the veneer of normal fluvial deposits it consists partly of unmodified moraine, partly of fluvial material reworked from glacial debris. In the vicinity of Grand Lake the recessional moraines control the direction of the river. On the margins of the lake the surface of the flood plain is made irregular by small hills of unmodified moraine and



FIG. 46.—Willow Creek, immediately south of Gold Run

Note the flood plain and well developed meanders. The vegetation in the foreground is sagebrush

by roches moutonnées which project upward through the detrital covering. On both sides of the valley the flood plain terminates against the moraines and alluvial fans of the tributary valleys or against the talus sheets derived from the oversteepened mountain walls. Along part of its course the Colorado shows a slight tendency to meander. In such places, as a result of frequent flooding, it has given rise to broad marshy meadows. However, on other parts of the flood plain it is actively lowering its bed, and flows several feet below the level of the flood plain. The accumulations of large glacial boulders give rise to many small rapids.

Stillwater Creek shows evidence of an unusual stream capture or diversion. Reference to the topographic map indicates that this stream has come to control most of the drainage of Pony Park at the expense of Trail Creek, which is one of the tributaries of Willow Creek. The evidence of this piracy is found in the swampy nature of the divide between these two streams, and in the marked rejuvenation of the upper course of Stillwater Creek displayed by two-cycle profile and large waterfalls. The cause of capture is by no means clear. Careful measurement of the two streams, from the Divide to their common local base level, which is the junction of Willow Creek and the Colorado River, shows them to be approximately equal in length. Furthermore, a comparison of the rocks over which they flow shows no serious difference in rock resistance. The profile of Stillwater is steeper in its northern part than that of Trail Creek. This sharpness of profile is in part a result rather than a cause of the "capture." A reasonable explanation could be assigned by postulating a temporary damming through ice or landslide, which might result in the ponding up and diversion of water into Stillwater Creek.

GENERAL SURFACE FEATURES

In this region the general surface features are controlled directly by the underlying structure of which there are three contrasting types, corresponding to the three great divisions of rock. The disordered crystalline rocks of the pre-Cambrian complex yield bold rounded hills and mountains. In the absence of glacial erosion the mountains are covered by a thick residual soil and are heavily forested up to the timber line. Here one finds a steep but nevertheless symmetrical topography, the landscape so characteristic of uplands of crystalline rocks dissected in a humid climate. At higher altitudes, where glacial erosion was active, the topography of the crystalline rocks is no less bold, but the rounded forms are concave upward rather than convex, and the smoothly curved summits are replaced by craggy pinnacles and arêtes.

In contrast to the bold scenery carved from the ancient resistant rocks there is the totally different topography produced by erosion on the effusive igneous masses. Over large areas the lava flows and tuff beds lie horizontal or else dip at a low angle. In such places erosion has etched the weaker rocks into a series of broad flat-topped mesas and cuestas. The edges of both present step-like alternations of vertical escarpments and steep treeless talus slopes. Their surfaces, particularly in the higher altitudes, are covered by rock debris, disintegrated to a coarse barren rubble. Soil is either scant or absent.

The western part of the area is underlain by a massive sedimentary formation of variable clastic strata which for the most part stand at high angles. Dissection by an adjusted drainage system has given rise to a series of interstream cuestas and hogbacks. Parkview Mountain, in the northwest of the area, consists of a sharp anticline dissected by cirques but otherwise little modified by erosion. The soil on the sandstone slopes is barren of clay and for many square miles supports sagebrush as its only vegetation. In the northwestern corner of the area the sediments are cut by long, massive porphyry dikes. The superior resistance of the dikes permits them to pursue their strike for long distances as vertical walls or steep ridges.

ECONOMIC GEOLOGY

METALS

No precious metals are now being mined in the area under discussion as far as can be ascertained. However, during the eighth and ninth decades of the past century there was a small production of gold (2, p. 11) and (12, p. 201) and silver. At that time the Front Range and the "Western Slope" were very carefully and thoroughly prospected. Prospect holes are encountered in nearly every section. The amount of energy consumed here in a vain search for precious metals is surprising. The sandstone walls of the middle cirque on the south side of Parkview Mountain display some twenty shallow shafts and tunnels. Holes have been blasted in every lava flow and in every tuff formation. The search for mineral in the crystalline rocks was better justified and resulted in the small production mentioned above. In spite of the seeming hopelessness of the quest, one or two prospectors yet linger in the area and carry on their search from year to year with a never-failing optimism.

The production of the last century came from several small ore deposits east of the Continental Divide from Lulu Pass south to Supply Creek. The inhabitants report that active mining ceased in this vicinity in 1888 or 1889. No figures of the amount of metal produced are available.

The mineralization which supported the industry is typically illustrated at an abandoned mine in the valley of Bowen Gulch, about seven miles upstream from its junction with the Colorado River. At this locality the country rock is an injection gneiss consisting largely of hornblende and biotite. This rock is cut by an irregular intrusion of green, fine-grained rhyolite porphyry which carries phenocrysts of sanidine. The intrusion of the porphyry was followed by fracturing, which had

little effect on the gneiss, but which brecciated the porphyry. Fracturing was succeeded by the mineralization, which occurred as a later stage of the igneous history. During mineralization the porphyry was silicified and the fractures partly healed by quartz. Quartz was also precipitated on the walls of the cavities as well formed prismatic and terminated crystals. The quartz was followed by the sulphides. Of the metallic minerals pyrite is the most abundant. This sulphide is disseminated through the silicified porphyry, partly following fractures in the introduced quartz, partly replacing it. The pyrite is a pale variety, crystallized in good cubes. The other metallics are cupriferous pyrite and copper sulphides, which are present in the same relation as the cubic pyrite. The last stage of mineralization brought in carbonate minerals, principally dolomite. The dolomite crystallized on the walls of the vugs from solutions of changing composition. Hence it shows a strongly banded structure and forms a layer which buries the terminated quartz crystals which formed on the walls of the vugs. The highest assay obtained from this deposit ran 17 ounces of silver and .2 ounces of gold per ton. Other similar deposits, west and north of this particular locality, frequently show argentiferous galena in addition to the minerals just listed, nevertheless their paragenesis is essentially the same. It is possible that when transportation problems are adjusted in this part of Grand County some of these mines may be reopened. Profitable exploitation of these deposits would necessitate careful management and efficient, economical concentration methods. The title to several deposits is retained by annual assessment work on the part of the owner.

On the south end of the Medicine Bow Range, section 21, T. 7 N., R. 76 W., a vertical shaft has been excavated in a down-faulted block of the Hugwater sandstone. At the time of the writer's visit, in the summer of 1921, the operators were away, so no information could be obtained concerning the details of the project.

In 1926 several claims were staked along Michigan Ditch and at Lake Agnes, following the discovery of sulphide mineralization. These claims have since been abandoned.

Somewhat later than the abandonment of the mines about the headwaters of the Colorado River, a placer mining operation was being carried on at the mouth of Gold Run. Here an alluvial fan of about five acres in extent was worked over to an average depth of six feet. The alluvial deposit is very heterogeneous in composition. Its most abundant constituents are large stream-rounded boulders up to ten inches in diameter. These boulders are crystalline rocks, lavas, and sandstone. With them are mingled gravels, sand, and clay particles of all sizes. A fine

black ilmenite sand is particularly abundant and it is most likely that the gold was associated with this sand in the placer deposit. It seems probable, furthermore, that both the gold and the black sand were set free by the weathering and erosion of the Denver arkose. The lenses of heavy residual minerals, which this sandstone contains, have already been mentioned. Thus the gold and ilmenite sand at Gold Run have passed through two cycles of erosion and deposition. In each case they were deposited

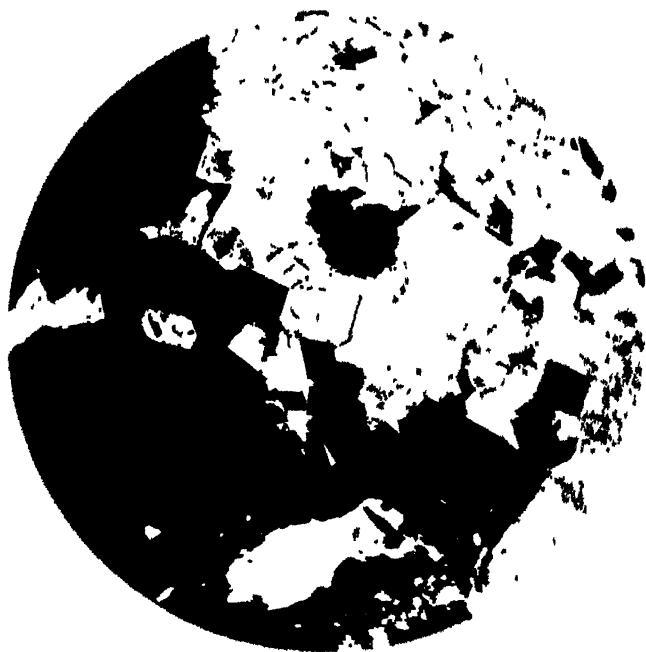


FIG. 47.—*Specimen L-37-C. "Ore" from Bowen Gulch*

Taken with combination of transmitted and reflected light. Magnification $\times 15$. Taken to show the sulphide mineralization. Note the sulphide following the contacts between the quartz crystals. Nearly all the sulphide is pyrite.

by streams of sufficient power and differential velocity to effect a concentration of the heavier minerals. Their ultimate source was doubtless in the crystalline rocks.

COAL AND HYDROCARBONS

In North Park subbituminous coal has been described by Beekly (*3*, pp. 93-116) from the Coalmont formation. Apparently the Coalmont

formation is in part the continuation and the equivalent of the Denver formation of Middle Park (3, pp. 61-66, and Pl. XII) although there is little similarity of lithology. The clastic material in Middle Park shows evidence of rapid deposition by swift-flowing streams and the plant remains bear the marks of vigorous abrasion. For this reason it seems quite natural that coal in this part of Middle Park is present only as occasional lenses of carbonaceous rather than bituminous sandstone. A few miles west of Willow Creek coal has been mined from time to time for local consumption.

At the boundary of sections 14 and 15, T. 4 N., R. 77 W., there occurs an isolated deposit of gilsonite (2, p. 19) and (3, pp. 117-118). This hydrocarbon is present in the sandstone where it fills fractures. A reasonable explanation for its occurrence would be the following. Heat was supplied either by the friction generated during the deformation of the sandstone, or else by the intrusion of the monzonite dikes, in sufficient quantity to distill the hydrocarbon from a carbonaceous seam or seams. The material, working its way upward along zones of weakness, solidified in the fractures of the sandstone.

The deposit was mined for several years in the first part of the present century, and several thousand tons were shipped by way of Granby. The material strongly resembles brittle bituminous coal. It fractures and fuses readily, but will only burn under a forced draft. It was used formerly in the manufacture of protective paints and similar compounds, but now the ranchers of the vicinity apply it as fuel in their forges.

WATER RESOURCES

The water supply of the region constitutes now the most valuable of the natural resources. The region, in consequence of its location, altitude and relief, is subject to a heavy though variable precipitation. On the other hand, the agricultural lands on the east side of the Front Range depend largely on irrigation for the necessary moisture. For this purpose the supply contributed by the east-flowing streams prove insufficient. To meet the situation water is now diverted from the western side of the Continental Divide, in the extreme northeast corner of Grand County and from the western side of the local divide formed by the Medicine Bow. The diversion is accomplished by a system of high altitude ditches, which are being extended every year. These artificial waterways are constructed at an elevation just sufficient to permit a flow over the Continental Divide without tunneling. Thus much water which would normally flow into Michigan Creek and the headwaters of the Colorado is

now diverted to the Cache la Poudre River. It flows on one side by way of Michigan Ditch and Joe Wright Creek, and on the other side by the Grand Ditch and Trap Creek. The construction and maintenance of these two ditches involve the expenditure of much energy and money. Each ditch is blasted from the rock or dug from the talus of steep glacial troughs. Hence a constant struggle is necessary to prevent the ditches from being filled by slide rock and to prevent them from slipping down into the valley. In addition, it is necessary to remove the snow from the entire system by hand in the early summer and to repair the winter's damage so that the beet growers in the neighborhood of Fort Collins may receive the water in July. During the summer of 1927 from twenty-five to thirty-five men were employed on the Michigan Ditch alone.

In Middle Park water is also diverted from the tributaries of the Colorado River by every rancher who possesses water rights. Most of this water is used during the middle of the summer in the growing of lettuce and general truck farming.

In spite of the many possibilities for the generation of hydro-electric power afforded by the steep gradients and favorable dam sites, no use is made of such opportunities, because of the brief season during which the power would be available, since the winters in this high altitude are long.

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THE GEOLOGY AND ORE DEPOSITS OF THE BUFFALO HUMP DISTRICT*

By RADCLIFFE H. BECKWITH

CONTENTS

Introduction.....	264
History.....	266
Topography and physiography.....	266
Geological history and structure.....	267
Summary.....	267
Sedimentary series.....	268
Stratigraphic relations of the schist and quartzite.....	268
Basic sills.....	270
Relation of schistosity to bedding.....	270
Evidence of age of the Idaho batholith.....	271
Magmatic stoping.....	271
Correlation of the sedimentary series.....	274
Gneiss.....	275
Relation of the gneiss to the quartzite.....	275
Relation of the gneiss to the schist.....	275
Basic sill in the gneiss.....	275
The granite, its derivatives and their effects on the quartzite.....	276
Syntectic products of granitic derivatives and schist.....	277
Time of folding of the sedimentary formations.....	281
Function of the quartzite in stopping the upward progress of the granite..	281
Faults.....	281
Sheeted structure.....	283
Age of the faulting and of the Idaho peneplane.....	283
Tertiary igneous intrusions.....	284
Ore deposits of Buffalo Hump.....	285
Country rock and its structural features.....	285
Vein system.....	286
Cross faulting.....	287
Character of the veins.....	287
Ore.....	288
Sequence of mineralization.....	288
Time and temperature of vein formation.....	290
Value of the district.....	292
War Eagle and Blue Jay properties.....	293
Blue Jay prospect.....	293
War Eagle Mine.....	294
Conclusion.....	295
Bibliography.....	295

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INTRODUCTION

The Buffalo Hump or Robbins District is situated in the Clearwater Mountains of western Idaho on the watershed between Salmon River and the South Fork of the Clearwater River (Fig. 1). The closest railway point is Grangeville. From Grangeville twenty-five miles of the road southward as far as Adams Camp can be covered in an automobile during the summer months. The remaining twenty-six miles of the road eastward to Humpstown was at one time used for freighting by wagon,

but is now in such a state of disrepair that it is fit only for travel on horseback. Another road from Grangeville follows the upland to the north of the South Fork of the Clearwater, passes through the old placer camps of Elk City and Oro Grande, and approaches Buffalo Hump from the northeast. This route is considerably longer than the one by way of Adams Camp, but a light car can be driven over it to within seven or eight miles of Humpstown.

The field work occupied two and one-half months during the summer of 1924. The district investigated includes 110 square miles (Fig. 2) in the roof of the Idaho batholith. An area considerably larger than that occupied by the

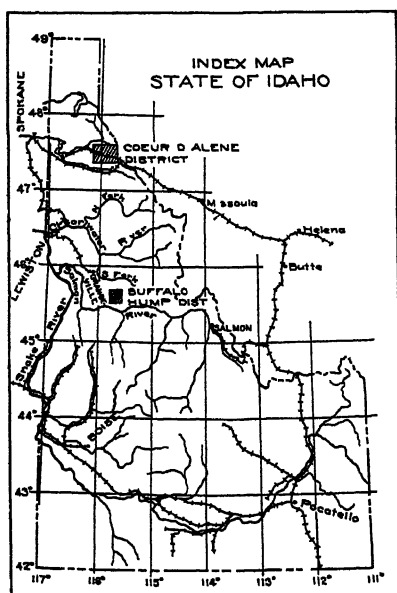


FIG. 1.—Index map of Idaho

Buffalo Hump vein system was examined in order to include the War Eagle and Blue Jay properties to the south near Salmon River and in order to ascertain the principal facts of the geological history of the region.

The writer is indebted to Mr. W. H. Day, Jr., of Dubuque, Iowa, for information about the War Eagle group of claims and for hospitality while visiting them. Thanks are also expressed to Professors J. F. Kemp and C. P. Berkey of Columbia University for valuable advice on field work and guidance in the preparation of the manuscript and to Professor R. J. Colony for aid in petrographic examination and interpretation.

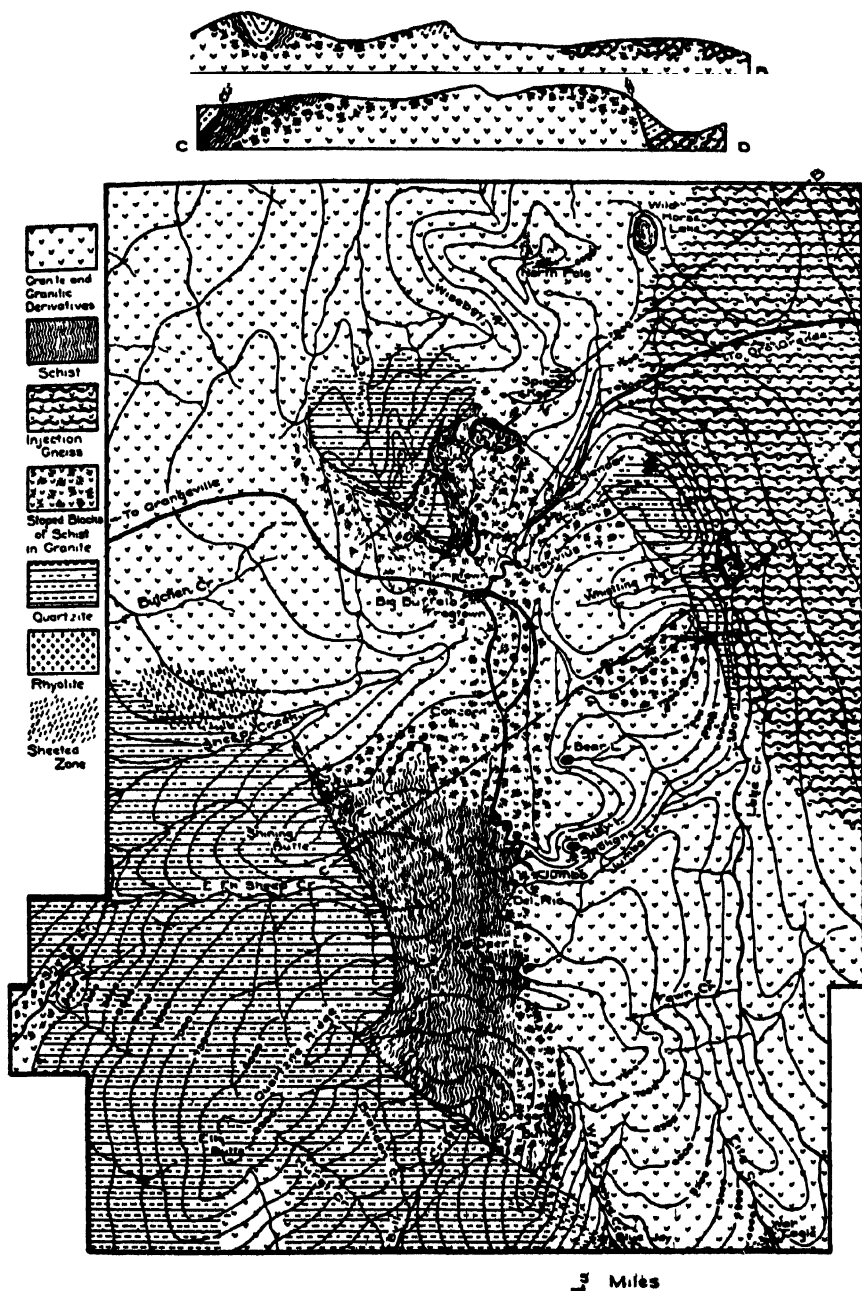


FIG. 2—Areal map of the Buffalo Hump District.

While in the field, the writer was aided in visiting the local workings by Mr. Peter Klinkhammer and Mr. A. F. Schultz, who are well acquainted with the quartz vein outcrops and the underground workings. The writer wishes to express his thanks to them and to Mr. Charles Schultz, Mr. Lauren Lennon, Mr. Edward Bettinson, Mr. Justin Smith and various members of the United States Forest Service for showing him hospitality at their camps and for supplying him with local topographic information.

HISTORY

The first quartz vein of the district was discovered in the fall of 1898 and a rush to the new gold field followed. In the early part of the present century there was a considerable population at Hump-town, Concord, Frogtown and Callender. Mills were set up on various properties and for some time the district turned out a fair production. Commercial operations continued for several years. The principal reasons for closing down were the expense of transport, the difficulty of working during the winter at an altitude of seven to eight thousand feet in a region of heavy snowfall and the lack of proper equipment for the treatment of an ore in which the gold and silver values are found in base sulfides.

The rich surface ores, which were not abundant because of extensive removal of material by glaciation, are now largely exhausted. Before profitable operations can again be opened, cheap transport in the form of a railway or a road suitable for heavy trucking must be provided. A survey for a railway along Salmon River has been made, but no construction work has yet been undertaken. A first class road is being built along the South Fork of the Clearwater, but at present it extends only a few miles above Grangeville.

TOPOGRAPHY AND PHYSIOGRAPHY

The best available map of the district is one compiled by the United States Forest Service for the use of its field force. The scale is one-half inch to the mile and the map gives only the main drainage lines and some of the more prominent peaks. Many of the topographic features were found to be incorrectly located, so that it became necessary to make rough compass triangulations to check the location of the points of primary importance before geological investigation was begun. Pacing was also used when the ground permitted it. The two principal triangulation stations used were Buffalo Hump and Oregon Butte, both of which were located and marked with stone monuments by the United States Geo-

logical Survey. On the accompanying map (Fig. 2) the locations of the major features check to within less than three-eighths of a mile. The contours were sketched from numerous aneroid readings taken in the course of triangulation and geological examination during the summer of 1924.

The Clearwater Mountains and the Salmon River Mountains to the south are a series of flat-topped ridges separated by deep canyons. The flat upland surface, which is usually described as the Idaho peneplane, lies at an altitude of about 7,000 feet around Buffalo Hump. From the summit of any of the peaks of the district, flat topped ridges at approximately the same altitude may be seen extending to the westward toward the Bitterroot Mountains in Montana. The flat-topped ridges of the Montana boundary are at a considerably higher altitude. To the south may be observed the peneplaned surface on the other side of Salmon River with the Seven Devils projecting conspicuously above it. To the westward there is a rapid descent until the old metamorphic rocks and granites are covered by the Columbia River basalt around Adams Camp and Grangeville. It is probable that some of the peaks, such as Buffalo Hump, Oregon Butte, Elk Butte and possibly Shining Butte, stood out as monadnocks above the peneplane.

The area mapped has been extensively glaciated and at present large snowdrifts last through the warmest summer around the two small lakes at the head of Ten Mile Creek. The ice was never of great enough extent to cap the district entirely, but there were large valley glaciers which extended down to an altitude of about 5,000 feet in Lake Creek and the East Fork of Sheep Creek. There are numerous cirques and glacial lakes caused both by overdeepening and by moraine dams. At the mouth of Crystal Lake solid rock outcrops only five or six feet above water level and not more than fifty feet laterally from the outlet. The lake is deep and the evidence is strongly in favor of a rock barrier. Fish Lake lies behind a mound of moraine deposited either because of overloading from the accession of the Whistling Pig glacier or by a temporary halt in the retreat of the main Lake Creek Glacier.

GEOLOGICAL HISTORY AND STRUCTURE

SUMMARY

A succession of pre-Cambrian schists and quartzites was invaded by the Idaho batholith in late Cretaceous or early Tertiary times. The sediments show extensive effects of injection, syntaxis, contact metamorphism and absorption. The granite also gave origin to the Buffalo

Hump group of quartz veins. Extensive faulting was followed by peneplanation. The region was then uplifted. After a long interval of erosion, during which canyons were cut into the upland surface nearly to their present depth, there was a period of minor intrusions followed by local glaciation.

SEDIMENTARY SERIES

The oldest rocks are a series of quartz schists composed of a base of quartz grains of more or less uniform size, ranging in diameter between .1 mm. and .2 mm., in which are plates of biotite and muscovite with closely parallel orientation (Fig. 3). There is no plication or contortion of the mica plates and the schist breaks in plane surfaces. The specimen examined also contains feldspars, which may either be primary constituents or may have been introduced from pegmatitic or aplitic dikes in the immediate vicinity. The presence of tourmaline showing its normal crystalline outline seems to support the second interpretation. The highly quartzose nature of the schist, its microstructure and stratigraphic considerations (to be considered subsequently), leave no doubt that it was originally a succession of sandy shales or graywackes. The base on which the sediments were deposited was not seen. The schist now rests upon granite, which has removed the lower part of the series in some places and has destroyed the whole of it in others.

Lying above the schist is a series of massive, white quartzites composed of uniformly graded, interlocking grains of about .5 mm. average diameter. The rock is extraordinarily pure and, in addition to quartz, contains only small quantities of muscovite and tourmaline. In several places within the quartzite, but near its base, there are small patches which superficially resemble conglomerate but, closely inspected, the fragments reveal themselves as very angular. Microscopic examination has shown that the material is not a conglomerate, but is instead a tourmalinized quartzite breccia.

STRATIGRAPHIC RELATIONS OF THE SCHIST AND QUARTZITE

There is no apparent stratigraphic break between the two sedimentary series. By gradual increase in the siliceous material and decrease in the micaceous material there is a transition from quartz schist through yellowish schistose quartzite to massive white quartzite. The schistosity is in all cases parallel to the bedding of the overlying quartzite. This change may be followed through several hundred feet stratigraphically on a glaciated surface near the point where the Bull Creek fault passes

across the northeast extremity of Quartzite Ridge. In the transitional schistose, yellowish quartzite there is distinct cross-bedded structure on a small scale. Essentially the same features may be observed on the first ridge to the west of Ten Mile Creek. In the syncline, in which is situated Buffalo Hump, the relations are somewhat different. Above the first massive quartzite are two bands of schistose quartzite or highly



FIG. 3—*Photomicrograph of typical quartz schist*

Showing the mosaic of quartz and very subordinate amounts of feldspar penetrated by plates of biotite and muscovite. $\times 65$ (crossed nicols).

siliceous schist with thicknesses of 200 feet and 300 feet respectively. The parallelism of the schistosity of the lower series to the bedding of the quartzite may be admirably observed at the southeast end of the Buffalo Hump syncline on a glacially smoothed surface, which is large enough to enable the observer to follow the change of strike through 90° .

BASIC SILLS

A series of basic intrusions older than the granite cut the schist and quartzite. The original igneous material has been very completely reorganized and the rock now consists of green hornblende, untwinned basic feldspar and very subordinate amounts of biotite. Titanite occurs as granular aggregates around cores of ilmenite. The intrusive bodies are tabular and are roughly parallel to the cleavage of the schist, or to the bedding when occurring in the quartzite. It is concluded that they represent diabase sills intruded before the formation of the present folds and before the invasion of the granite by which they are cut.

RELATION OF SCHISTOSITY TO BEDDING

The basis sills frequently show well developed schistose structure. In all observed instances it is parallel to the bedding of the quartzite or to the schistosity of the lower series. The parallelism of the schistosity of the lower series and the diabase sills to the bedding of the quartzite might be explained as a case of metamorphism by a vertically superimposed load such as has been described by Daly¹ (3, pp. 44-49) from the Shuswap Terrane of pre-Cambrian age in British Columbia and by W. J. Miller (9, p. 597) from the Grenville of the Adirondacks. The rise in temperature in the overlying beds during the upward advance of the granite batholith would be a factor tending to aid the development of schistosity under vertically superimposed load, but the time of formation of the sharp folds, with dips up to 90° which are now found in the schist and quartzite, is not known. The folding may have taken place long before the batholithic intrusion began or only shortly before the granite reached its present position. The possibility of the development of cleavage in the usual manner by stresses applied in a direction closer to the horizontal than to the vertical cannot be excluded, for the presence of the folds is evidence that these stresses have been present. A possible interpretation is that the schistosity was developed by load metamorphism when the pre-Cambrian series and the diabase intrusions lay in a horizontal position, while the folds were developed later. This interpretation is not advanced as necessarily being the correct one, but it fits in very well with the field evidence. The schistosity of the lower series is parallel to the bedding of the overlying quartzite, which is in marked contrast with the observations of Leith (6, p. 127), who finds, in the

¹ Throughout this paper the bibliographical references are designated by an italicized number in parentheses. The author and title of the paper may be ascertained by reference to the corresponding number in the Bibliography.

Lake Superior district, that schistosity is developed parallel to the axial plane of the fold.

EVIDENCE OF AGE OF THE IDAHO BATHOLITH

The older metamorphic rocks have been extensively invaded by the granitic rocks of the Idaho batholith. There is no evidence in the Buffalo Hump District as to its age, except that it is younger than the schist, quartzite and diabase, and older than the Idaho peneplane and a series of basaltic dikes which may be of the same age as the Columbia River basalt. In the southern part of the batholith, near Hailey, on Wood River, it has been shown that the intrusion is certainly post-Carboniferous (7, p. 79). Umpleby (12, p. 43) assigns to it a late Cretaceous or early Tertiary date. Calkins and Emmons (1, p. 11) found that the Phillipsburg batholith located some fifty miles east of the Idaho batholith cuts sediments of Colorado age. In the Phillipsburg quadrangle other intrusions of apparently the same age are overlain by sediments of Tertiary age. Since the two batholiths are probably of the same age, it is quite probable that the Idaho batholith was intruded in late Cretaceous or early Tertiary times.

MAGMATIC STOPING

The Buffalo Hump District provides some excellent examples of extensive displacement by the batholith of rocks which were originally sediments. The general absence of a covering of mantle rock and the topographic features give extraordinary facilities for direct observations. The steep-sided valleys and cirques give large, nearly vertical exposures and with the adjacent upland surfaces make it possible to study the relations of the various geological units in three dimensions. Starting from the upland one can descend into a valley and actually see in its side what is beneath a given formation instead of having to make inferences from what can be seen on a nearly level surface.

The oldest rocks of the district are the schists. If the deduction be correct that the cleavage of the schist series is parallel to the bedding of the sedimentary series from which it was formed, the greatest thickness is present to the west of the Jumbo Mine, where the schist dips to the westward beneath the broad syncline at the head of the East Fork of Sheep Creek and at the northern end of Quartzite Ridge. Here the width of the outcrop, measured across the strike, is some 7,000 feet. The dips vary from 40° to 60° and the average may be conservatively placed at 45°. The thickness is, therefore, about 4500 feet. This may

be taken as a minimum figure, since the base on which were deposited the sediments from which the schist series was derived, is not present. Instead the schist rests upon the granite with clearly intrusive contact well exposed on a bare, glaciated surface sloping 30° to 45° into the head of Jumbo Creek. Dikes of granite and granitic derivatives extend outward into the schist. In addition, there are a few blocks of schist within the granite. The band of granite with schist inclusions is here very narrow.

To the east of the Buffalo Hump synclinal area of quartzite the zone of transition from massive granite to undisturbed schist is much wider and is well exposed both on the glaciated west wall of Lake Creek Canyon and on the flat surface around Buffalo Lake. Near the bottom of the canyon there is massive granite containing blocks of highly contorted schist, often so thoroughly granitized and impregnated by magma as to be hardly recognizable. In some cases the only remnants of the schist are a few parallel bands of biotite in the granite. Higher in the canyon wall is a zone of schist cut by a criss-cross pattern of pegmatite, aplite and granite dikes. Still higher in the vicinity of Buffalo Lake there are numerous dikes which have extensively granitized the schist, with introduction of feldspathic material and partial conversion of the biotite of the schist to hornblende and epidote. In this region there is accordance of strike across intrusions and the schist is essentially in place.

An attempt has been made to show these relations graphically on the map. Where the schist is in place, it is shown by continuous wavy lines, which indicate the strike of the schist. Where the schist occurs as blocks within the granite, it is shown as patches of wavy lines within the granite symbol. No boundary lines have been used for magmatically stoped contacts. Since to examine every exposure would have consumed an excessive amount of time, it is likely that some of the areas mapped as blocks of schist embedded in granite are schist essentially in place, but extensively cut by dikes. Where this relation was definitely recognized, the continuity of the schist lines is interrupted only by the granite symbol.

In some localities the schist is entirely absent between the granite and the quartzite. Three hypotheses may be suggested to explain its absence:

1. Overlap.
2. Faulting.
3. Removal of the schist by the magma.

It is to be noted that the schist series is at least 4500 feet thick to the west of the Jumbo Mine, while only six miles to the north, near

the Wiseboy Mine, it is entirely absent. If there were an erosional unconformity of sufficient size to cause the quartzite completely to overlap the schist in the northern exposures, one would expect to find both discordance of dip and strike between the schist and the quartzite and also a basal conglomerate beneath the quartzite both to the west of Buffalo Lake and at the northeast end of Quartzite Ridge. Neither is present. This and certain other features described below make it impossible to explain the absence of the schist between the granite and the quartzite by overlap.

The only place where there is evidence of the granite and quartzite having been brought into contact by faulting is near the mouth of Whistling Pig Creek. To the south of the Wiseboy Mine both are exposed on a bare slope varying in inclination from 30° to 90°. No crush zones or bands of fault breccia separate them. Instead the quartzite lies upon massive granite, which sends out dikes a short distance into the quartzite. There are a few occurrences of fairly large blocks of quartzite well within the granite, such as on Ten Mile Creek and on the ridge to the northwest of the War Eagle Mine, approximately half a mile from the lower tunnel and 800 feet above it. In these two cases it was not possible to look at the bottom of the blocks, but the contacts with the granite showed no evidence of faulting. The block of quartzite on top of Spion Kop, however, stands out as a sharp peak and the contact beneath may be examined on steep surfaces. It has much the same features as the one south of the Wiseboy Mine with the quartzite lying on massive granite and penetrated by dikes fingering off from the main mass of the granite. In addition there are a few small rounded blocks of quartzite within the granite immediately below the contact. Several hundred feet below the base of the quartzite in the north wall of Crystal Lake there are a few sub-angular blocks of schist embedded in the granite. Their maximum dimensions vary up to twenty feet. Although the foliation and general structure of the schist have been preserved, the blocks have been extensively epidotized.

It seems hardly worth while to review here all that has been written on the subject of magmatic stopping, absorption and its effect on the magma and subsequent differentiation. In conclusion it may be said that the occurrence of blocks of schist and quartzite embedded in massive granite gives strong evidence that magmatic stopping has taken place. The lack of another satisfactory explanation to account for the presence of 4500 feet of schist between the quartzite and granite in one place and its total absence only six miles away, together with the evidence of magmatic stopping and partial absorption of blocks by the granite magma,

gives strong evidence that the magma made room for itself by displacement of the surrounding rocks.

CORRELATION OF THE SEDIMENTARY SERIES

An attempt was made to work out the structure of Quartzite Ridge, but the roughness of the ground, which made pacing impossible, caused the attempt to be abandoned. Fairly reliable pacing measurements were made across the Buffalo Hump syncline where a thickness of 1000 feet of quartzite is present. This should be taken as a minimum. It is highly probable that all of the quartzite series is not present in the syncline, since the next formation above the quartzite is not seen anywhere in the district. Reliable measurements of the thickness of the quartzite might be obtained around Gospel Mountain and Moore's Ranger Station, fifteen miles to the westward, where it was seen by the writer. The schist series also occurs in this vicinity, especially in Slate Creek Canyon, where it has been extensively injected to form a gneiss.

There is no conclusive evidence in the district as to the age of the schist and quartzite series. The lack of fossils, the great thickness, the thoroughly metamorphosed character and the position immediately above the granite, lead to its classification as pre-Cambrian of the Belt Group. The closest locality in which the thicknesses of the various members of the Belt Group are known is the Coeur d'Alene District, but rocks of somewhat similar character, which are classified as Beltian, are known to the northwest in Latah County, to the eastward in the Bitterroot Mountains, and in Lemhi County. The following tentative correlations may be made on the basis of lithological similarity:

<i>Buffalo Hump District</i>	<i>Coeur d'Alene District</i>
Quartzite 1000 feet (top not seen)	Revett quartzite 1200 feet
Schist 4500 feet (base not seen)	Burke formation 2000 feet
	Prichard slate 8000 feet (base not exposed)

The Burke formation is composed of fine-grained sandstones, flagstones and shales showing shallow-water features throughout. The upper part of the Prichard slate has very much the same lithological character. It is material of this kind which, upon metamorphism, would change to a highly quartzose schist such as that of Buffalo Hump.

GNEISS

In addition to the units described, there is also a gneiss of rather widespread occurrence formed by the injection of pegmatitic material from the underlying granite between the leaves of the schist. This relation has been represented on the map by pairs of continuous wavy lines passing between the V's of the granite symbol. The direction of the lines does not represent the strike of the banding of the gneiss.

RELATION OF THE GNEISS TO THE QUARTZITE

Stratigraphic evidence bearing on the origin of the gneiss is best illustrated by the section along C-D (Fig. 2). A strip of quartzite dipping to the west is found faulted down against the granite to the west of Lake Creek. Beneath the quartzite appears a gneiss composed of narrow bands of biotite and muscovite alternating with bands from 2 mm. to 5 mm. wide of orthoclase, albite, microcline and abundant quartz showing marked strain effects. Here the gneiss is in the stratigraphic position occupied by 4500 feet of schist found conformably below the quartzite at the head of the East Fork of Sheep Creek. It is highly improbable that there could be, in only five miles, an overlap of the quartzite onto an older gneiss in such a manner as to omit the whole of the sedimentary series represented by the schist.

RELATION OF THE GNEISS TO THE SCHIST

The banding of the gneiss is not continuous over large areas nor does it show any consistency of strike. Outcrops are found where the micaceous bands fade out laterally into normal granite or some granitic derivative such as pegmatite or aplite. Large blocks of readily recognizable schist are found embedded in and completely surrounded by granite. Many of these xenoliths are typical schist only in the center. When traced a few feet laterally, the schist leaves open and dovetail with pegmatite veinlets and the rock becomes a typical banded gneiss. Farther away from the center of the xenolith the micaceous bands fade out into massive igneous rock. These relations lead to the following interpretation:

The granite magma stopped its way upward into the schist and pried off numerous blocks, some of which were completely absorbed. Others remained in such a state as to be recognizable as schist. Still more of the schist, both in the form of stopped blocks and masses held in place by support from above, was subjected to extensive impregnation and *lit-par-lit* injection by material of aplitic and pegmatitic nature, some

of which still remains as dikes and patches which finger off laterally between the micaceous bands of the gneiss.

BASIC SILL IN THE GNEISS

Within the gneiss, a short distance above Fish Lake, was found a schistose black rock composed almost entirely of brown biotite, but containing a few grains of quartz and ilmenite. It forms a tabular mass, four to six inches thick, lying parallel to the banding of the gneiss and extending laterally for ten feet. Its shape is such as to indicate that it occurred as a sill within the original schist. A few pegmatite veinlets have penetrated the schistose parting, but there has been no intimate injection and impregnation as in the case of much of the normal quartz schist. It is believed that this dark mica schist was once a basic sill intruded into the original sediments. It probably belongs to the same phase of igneous activity as the basic sills found in the schist.

THE GRANITE, ITS DERIVATIVES AND THEIR EFFECTS ON THE QUARTZITE

The granite of the batholith varies in composition. A specimen collected near the mouth of the Jumbo lower tunnel is a normal quartz monzonite with muscovite and biotite. Another specimen, from the War Eagle claim, is a granite composed of quartz, orthoclase and microcline with minor amounts of albite and muscovite. There are also pegmatites and aplites, some of which occur as well defined dikes and lenticular masses with sharp boundaries cutting the granite and the metamorphics. When the pegmatites are in contact with the granite, there is not, in some cases, any well defined boundary between the two, but instead there is a gradual change in the relative proportions of the minerals and size of the individual mineral grains. The contacts of the granite and its apophyses with the quartzite are usually sharp. The quartzite seems to have resisted magmatic invasion much more effectively than the schist. Stopped blocks of quartzite found within the granite show slight absorption effects, such as rounding of corners, but there has apparently been no wholesale reorganization of material in place. Absorption progressed by solution and the diffusing away of dissolved material, rather than by reorganization of minerals with recrystallization near the point of origin, as in the case of some of the rocks described below.

SYNTHETIC PRODUCTS OF GRANITIC DERIVATIVES AND SCHIST

Rocks produced by reaction between schist and granitic derivatives are exposed in the cuts of the road from Callender to Humptown near the base of the zone of magmatically stoped blocks. Here a steeply inclined, tabular mass of coarse pinkish rock grades outward into a coarse gray rock with abundant hornblende and only a small amount of quartz. The



FIG. 4.—Photomicrograph of aplite in contact with the orbicular granite
ol=oligoclase; q=quartz. $\times 25$ (crossed nicols).

mineral grains along the surface of contact of the two types are intimately interlocked. Several feet outward from the lightest rock there is a gradual change from the coarse gray rock to a finer-grained, grayish-brown rock. The hornblende decreases in quantity outward and gives way to biotite. Three or four feet from the lightest rock the gray rock is typical mica schist.

Microscopic examination of the light rock showed it to be a granular pegmatite composed of perthite and soda orthoclase with quartz. Garnet,

titanite, biotite, muscovite and a dark mineral, probably magnetite or ilmenite, are minor constituents. The coarse gray rock proved to be of the composition of a monzonite bearing minor quantities of quartz, but has some unusual mineralogical and structural features. Apatite and titanite are much more abundant than is usual in rocks of purely igneous origin. The quartz grains show marked strain effects. No definite order of crystallization of the constituent minerals can be formulated.



FIG. 5.—Photomicrograph of the contact of a spheroid of the orbicular granite and its matrix

Showing the line of mica flakes parallel to the contact. $\times 65$ (crossed nicols).

Hornblende does not usually occur in its own characteristic crystalline form and is intimately associated with biotite, which, in many cases, has ragged borders suggesting absorption. The hornblende also acts as a host for quartz and feldspar. These features lead to the conclusion that the rock is not a product of primary crystallization from the molten condition, but was formed by introduction of feldspathic material into the schist from the pegmatite, accompanied by partial absorption of the

original biotite, which later recrystallized as hornblende. It is probable that the garnet in the pegmatite is also a syntectic product. Examination of other specimens with the same field relations taken from the same locality leads to their classification as quartz-diorite and granodiorite. They have the same micro-structural relations as the monzonite.

The road from Humpstown to Callender passes over a patch of orbicular granite on the south side of the head of Lake Creek. The orbicular



FIG. 6.—Photomicrograph of gray matrix of the outer edge of the orbicular granite showing the characteristic quartz and feldspar mosaic of the quartz schist. q=quartz; f=feldspar; bi=biotite; sp=titanite. $\times 25$ (crossed nicols).

rock is a mass ten to fifteen feet wide, 300 feet long, striking N. 10° W. and standing nearly vertically. At several points in the center of the orbicular mass are lenticular patches of fine-grained, white aplite composed almost entirely of oligoclase, albite-oligoclase and quartz with minute quantities of biotite, muscovite and apatite (Fig. 4). By gradual change of mineral composition the aplite passes outward into a zone of

coarse-grained dark-gray granitoid rock in which are embedded white spheroidal masses varying in size from 2 cm. to 4 cm. The spheroids are sometimes nearly in contact with only 2 mm. of the darker matrix separating them and often have dark cores up to 1 cm. in diameter, composed largely of biotite and hornblende. At the outer edge of the outcrop the spheroids are embedded in a brownish black, highly micaceous matrix which, by a decrease in the number of spheroids, passes into a contorted, fine-grained, dark-brown mica schist.

The white material of the orbicules is composed almost entirely of oligoclase, which, in some cases, is in optical continuity for distances of 1 cm. The coarse gray matrix is of the same nature as the syntectic quartz-diorite described above and has the same micro-structural features. A thin section across the contact of one of the spheroids and the dark matrix near the outer edge of the orbicular zone shows abundant mica along the contact. All of the flakes are very nearly parallel to the margin of the orbicule (Fig. 5). The same slide contains a field (Fig. 6) with the characteristic mosaic pattern of the typical quartz schist. It is believed that the orbicular granite was formed in the following manner:

A large block of schist, held at a high temperature by the molten granite immediately below and by the numerous surrounding dikes, was cut by an aplite dike abundantly charged with mineralizers. By partial solution of some of the material of the schist and reaction between the aplitic material and schist the zone of material now occupied by the orbicular granite was converted into a spongy mass. From this the feldspars began to crystallize from a few centers, sometimes about a core of micaceous material from the schist and sometimes about a grain of feldspar. From these centers the feldspar grew outward and, by its force of crystallization, pushed the micaceous materials outward as indicated by the orientation of the mica flakes with their large faces parallel to the contact of the feldspathic spheroids.

The principal mineralogical change, which apparently took place, is the conversion of biotite to hornblende. This is a rather unusual change. A much more common one in igneous rocks is the alteration of biotite to chlorite, which, it is believed, goes on during the end stages of magmatic cooling or under surface conditions. If the process outlined above be the true interpretation, the expectation would be that fairly high temperatures would be attained and that hornblende would be formed at the time of reaction between aplite and schist by actual solution of biotite and recrystallization of some of the dissolved material as hornblende,

as well as by alteration of biotite in place. It is likely that garnet and titanite were formed in essentially the same manner by the reorganization of material already present in the schist. The pure quartz-feldspar composition of the aplite provides strong evidence against the extensive introduction of hornblende, garnet or titanite from the invading magmatic material.

TIME OF FOLDING OF THE SEDIMENTARY FORMATIONS

The folds seen within the old metamorphic series are undoubtedly older than the end stages of consolidation of the granite. In the structures followed out, such as the syncline at the head of the East Fork of Sheep Creek and the northwesterly pitching syncline and anticline of Buffalo Hump, the dips are generally high and are sometimes almost vertical. If there had been extensive orogenic movements during the last stages of intrusion of the batholith, it is highly probable that the crystals of the granitic areas without xenoliths would show a definite orientation and that there would be more or less banding of the granite. These two features are conspicuously absent.

FUNCTIONS OF THE QUARTZITE IN STOPPING THE UPWARD PROGRESS OF THE GRANITE

The schist series seems to have offered comparatively little resistance to the stoping process and in some places it has been entirely removed from beneath the quartzite, which acted as a much more resistant unit and was not extensively penetrated by dikes. It is partly to the protection of the overlying quartzite that the remnants of schist owe their preservation. It is probable that the large area of injection gneiss in the northeast corner of the map represents only the upper part of the schist which was protected by a cover of quartzite. The quartzite prevented dikes from penetrating very far upward and prying off blocks. Angular fragments of quartzite were found in the surface material along the Oro Grande road in the northeast corner of the map. The débris is here rather heavy, but it is probable that ledges exist below the surface and that the quartzite extended from the area to the west of Lake Creek over the whole of the gneiss area at the time of the cooling of the granite.

FAULTS

A series of normal faults of considerable displacement were formed after the consolidation of the granite. There are three such faults of

major importance. The Whistling Pig fault strikes N.N.W., roughly parallel to Lake Creek. The westward-dipping quartzite has been carried down against the granite. No accurate measurements of the throw are available because the fault passes out into the granite across a magnetically stoped contact at both ends. A minimum value for the displacement may be estimated. The west side of the fault on the ridges to the north and south of Whistling Pig Creek is in the zone of abundant blocks of schist in the granite. The general impression gained in going over the ground was that the schist was very abundant. It is possible that some of the blocks were held in place as roof pendants. No blocks of quartzite were found here. It is safe, therefore, to assume that the base of the quartzite was above the present tops of the ridges. The base of the quartzite in the downthrown block is now 1500 feet below the top of the ridge where it is crossed by the fault. Since the quartzite dips to the west, it is safe to take 1500 feet as a minimum value for the throw in the immediate vicinity of the place where the measurements were made.

Another normal fault of major importance strikes northwest across the head of Bull Creek. To the northwest it passes into the quartzite in the East Fork of Sheep Creek and to the southeast it passes over a stoped contact. The displacement was not all along one major plane, as it has been represented on the map. To the south of the line along which the quartzite is brought into contact with the granite and schist on the ridge extending southward from Oregon Butte, the granite and quartzite show extensive sheeting parallel to the main fault. The sheeting and a series of cross joints give origin to a conspicuous topographic feature. Roughly tabular masses twenty to fifty feet wide bounded on three sides by almost vertical faces project from the mountain side and, in some instances, there is also a vertical back slope, leaving a rectangular column ten to twenty feet high. The same feature may be seen on the east slope of the West Fork of Crooked Creek, where the main jointing, however, strikes almost due east and west, and it is not likely that the jointing is related to the Bull Creek fault.

The aggregate displacement of the fault is large and probably of the magnitude of several thousand feet. The quartzite to the south of the fault is extensively crushed and no attempt was made to work out its structure. The schist has a steep westerly dip in the head of Bull Creek and the quartzite is brought into contact with a stratigraphic horizon several thousand feet lower. In the bottom of Bull Creek there has been movement on a second fault, which passes into the main fault, leaving a triangular mass of quartzite between them.

The Shining Butte fault is almost parallel to the strike of the schist and quartzite. The former is considerably disturbed for a quarter of a mile to the east of the line of principal displacement. The aggregate throw is probably not more than several hundred feet.

SHEETED STRUCTURE

Sheeted structure occurs in several localities and takes the physiographic expression of columns and tabular masses such as were described above in connection with the sheeted zone to the south of Oregon Butte. An extensive sheeted zone north of Sheep Creek is shown on the map, the direction of the lines indicating the strike of the sheeting planes, which stand nearly vertically. Another sheeted zone occurs on the War Eagle group of claims, where a series of steeply dipping parallel fractures strike N. 65° E.

AGE OF THE FAULTING AND OF THE IDAHO PENEPLANE

The faults are all younger than the granite. Most of the displacement along them took place before the erosion of the Idaho peneplane. The quartzite to the north of Whistling Pig Canyon underlies a flat-topped ridge, which is a part of the peneplane or a remnant above it. The fault makes no well-defined topographic break in the top of the ridge. The age of the peneplane, however, is a disputed point. The majority of the geologists who have worked in western Idaho give its age as Eocene, but it is sometimes placed as late as Miocene. The whole matter is well summed up in a paper by Mansfield (8, pp. 472-487).

The information collected by the writer favors a pre-Miocene date. A critical point in the question is the age of the Columbia River basalt and this will first be considered. A number of fossil leaves were collected in a stream-deposited bed of volcanic ash in the basalt three miles from Grangeville along the road to Adams Camp. These were submitted for identification to Dr. A. L. Hollick of the New York Botanical Garden. None of the specimens were identified as belonging to a previously described species, although some of them appear to be similar to certain plants in the Eagle Creek formation, which is regarded as Oligocene by R. W. Chaney (2, pp. 115-118). Dr. Hollick considers that the flora as a whole is suggestive of that described by F. H. Knowlton (5, pp. 721-736) from the Payette formation, which, on the basis of its flora, is thought to be Upper Miocene. Although the plants collected by the writer do not give conclusive evidence on the age of the Columbia River

basalt around Grangeville, Dr. Hollick's tentative conclusions on the stratigraphic horizon of the flora fit in well with the information collected from other localities. The age of the Columbia River basalt is generally conceded to be Miocene on evidence consisting mostly of fossil plants in interbedded sediments. The specimens were collected from various points and most of them were determined by Knowlton (4, pp. 103-104) and Merriam.

The undulating upland surface of the region for some miles around the Buffalo Hump district is profoundly dissected by deep canyons containing the principal streams. This feature may be seen on any clear day from the top of Oregon Butte or any of the other more prominent peaks. Farther to the west, near Adams Camp, the distinction between the upland surface and the canyons is not so well marked, but the basalt here lies upon an eroded surface of the granite. It is apparent that, whether it belongs to the cycle represented by the peneplane or to the succeeding cycle of canyon erosion, the basalt is younger than the erosion surface.

TERTIARY IGNEOUS INTRUSIONS

Data which may bear on the age of the peneplane are found within the Buffalo Hump District. In the bottom of the West Fork of Crooked Creek on the Blue Jay claim at an elevation of 3500 feet there are several basalt dikes cutting the granite. They are fine-grained and once carried olivine phenocrysts, which have been altered to talc. There has been no noticeable shearing, such as that which affected the pre-Cretaceous diabase intrusions. The dikes are of near-surface type and of essentially the same petrographic character as surface flows. It is apparent, therefore, that the creek had eroded nearly to its present level at the time of the intrusion of the basaltic magma. It is possible that the dikes are a phase of the period of igneous activity represented by the Columbia River basalt, which occurs in typical development only twenty miles to the west. If this assumption be correct, the conclusion is reached that the Idaho peneplane had been formed, uplifted and dissected to a depth of some thousands of feet before Miocene times.

In addition to the basalt dikes there are other minor intrusions younger than the granite. Gray andesite dikes bearing small amounts of quartz, which shows marked resorption effects, were encountered underground in the Jumbo and Spokane workings. They were not seen in place by the writer because of the caving-in of the tunnels. About 1000 feet to the southeast of the St. Louis tunnel a dike of similar nature outcrops. It

varies in width up to twelve feet and was traced for 900 feet in the direction of N. 68° E. There is another shorter dike 200 feet to the eastward striking roughly parallel to the first one. Dacite porphyry dikes are known on the War Eagle claim and are of rather common occurrence in Salmon River Canyon.

On the eastern side of Sheep Creek, a mile below the mouth of East Fork, is an ellipsoidal body of rhyolite approximately half a mile long. Its major axis extends in a northeasterly direction. The contact cuts across the quartzite and granite with schist inclusions. The stratigraphic horizon, therefore, is essentially the base of the quartzite. The rhyolite is fine-grained, light-colored and shows distinct flow structure. Quartz phenocrysts are not abundant and one specimen collected was typical felsite. Although the rhyolite is of extrusive type, the body is not a flow, but the upper part of the feed pipe of a volcanic cone. Near the northwest margin the rhyolite is cut by an andesite porphyry dike twenty feet wide, which may be traced for several hundred feet in the direction N. 6° W. The dike stops abruptly at the contact with the granite.

The age relations of the various minor intrusions described above are not apparent from the field information. The occurrence of surface types such as felsite and rhyolite in contact with the Cretaceous or early Tertiary granite several thousand feet below the Idaho peneplane indicates that these rocks are considerably younger than the peneplane. It is probable that the andesite dikes encountered in the Spokane and Jumbo tunnels and the dacite porphyry dikes on the War Eagle claim belong to the same period of igneous activity as the rhyolite plug. Whether the basalt dikes on the Blue Jay claim are of this age or whether they belong to an earlier or later period of igneous activity is not known. It is suggested that they are of the same age as the Columbia River basalt.

ORE DEPOSITS OF BUFFALO HUMP

On the upland to the east of Buffalo Hump and its extension three and a half miles southward, is a group of quartz veins which at various points carry pyrite, sphalerite, galena and chalcopyrite.

COUNTRY ROCK AND ITS STRUCTURAL FEATURES

The country rock of the area in which the vein system is situated consists principally of granite and granitic derivatives, such as pegma-

tite, aplite and alaskite, but there are abundant inclusions of schist and in some places the schist may be essentially in place. Lack of time prevented following out in detail the strike of the schist to determine its structural condition after invasion by the granite. Consequently the areal map shows extensive areas as stoped blocks of schist in granite, which may be schist in place, but cut by so many dikes as to give the impression of predominant granite. It is very likely that the two ridges to the north and south of Whistling Pig Canyon are of this nature. The general features of the structure which caused the concentration of the ore-forming solutions are suggested by the areal map and the section along C-D (Fig. 2). To the westward the schist dips steeply beneath the quartzite. A band of granite without inclusions extends northward from the vicinity of Bear Lake into the head of Whistling Pig Canyon. To the east of this belt is a roof pendant of schist with abundant granite. It would thus appear that the vein system is in the western part of an elongated cupola with northerly trend. This is not so apparent in the southern part of the vein system around the Spokane, Jumbo and Del Rio mines. It is probable, however, that the schist once extended downward to a lower level around the mouth of Jumbo Creek, but has been entirely removed by erosion.

VEIN SYSTEM

The pattern of the vein system is shown on the accompanying map (Fig. 7). A week was spent in going over the ground with Mr. Peter Klinkhammer, who has an excellent first-hand knowledge of the workings. Rough measurements were made with compass and pacing and were checked by the map compiled from the survey of the camp by Hill and Tillson. In the case of patented claims the locations are fairly accurate. Veins have been mapped as continuous only when they are exposed at the surface, in trenches, or underground, at intervals of 50 feet to 300 feet. Where the exposures appear at greater intervals, the probable extension of the vein has been represented by a dotted line, with individual trenches in which vein quartz was encountered, shown by short dashes perpendicular to the dotted line. The local names of the veins are given only where the veins are continuous from the location at which the name was originally given. The various exposures of vein quartz were from six inches to seven or eight feet wide. Four feet may be taken as a fair average. A width of thirty feet of quartz is reported from underground workings at the Concord Mine, but the shaft could not be entered and the writer saw only surface exposures.

The strike of the veins varies from N. 20° E. to N. 30° E. The St. Louis and San Francisco varies only three or four degrees from N. 22° E. over a distance of nearly a mile. The western members of the group dip steeply to the westward and those on the east side have an easterly dip. The Dewey stands almost vertically. No observations could be made on the dip of the Concord vein which shows only a few stringers at the surface around the shaft. Men who worked underground when the mine was in operation, report a dip to the east.

CROSS FAULTING

There are indications of cross faulting as shown by offsets, always to the left. The offset to the south of the Monte Cristo might be interpreted as due to other causes than faulting. The northernmost trenches on the St. Louis and San Francisco vein are more than a thousand feet from the closest ones on the Monte Cristo. The ground between them is well exposed over the major portion of the distance with only a few boulders and logs on the surface of the solid rock. It is likely, therefore, that there are two separate veins which pinch out in the same general vicinity. In the case of the offset on the Mother Lode or Concord vein, where the exposures to the north and south of the offsets are closer together, the evidence of cross faulting is more convincing.

CHARACTER OF THE VEINS

The gangue of the veins is milky white, coarsely crystalline quartz. Druses and cavities are fairly common. Crustified structure is not usually well developed, but several specimens were collected in which there is rude banding. The contact with the wall is usually sharp, and the vein and wall rock are often separated by a thin film of gouge designated by the local miners as "talc." This kind of contact, however, is not present everywhere. An offshoot was observed underground in

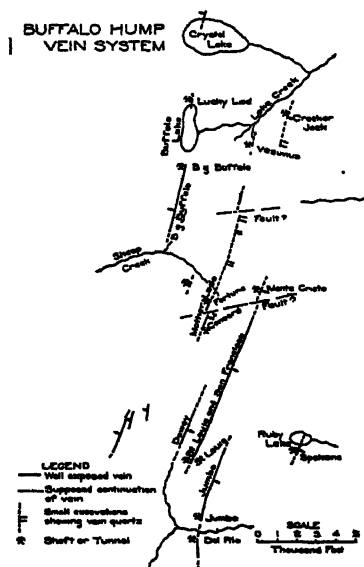


FIG. 7.—Buffalo Hump Vein System.

the Del Rio Mine in which quartz with sulfides forms an irregular transition to massive granite. The same condition, it is said, prevails in some of the underground workings at the Concord Mine, where there is no well defined hanging wall. A specimen collected from the vein in the St. Louis Tunnel contains a fragment of granite wall rock sericitized and impregnated with sulfides. The wall rock is usually sericitized and silicified, but is not extensively impregnated with sulfides. In some cases the veins split into a number of ramifying stringers, but this is rather uncommon. Where the veins have been well exposed at the surface, as in the case of the Jumbo, St. Louis and San Francisco, Dewey, Big Buffalo and the three unnamed short veins in the southwest corner of the group, there is remarkable constancy of width.

ORE

Pyrite, sphalerite, galena and chalcopyrite occur in the quartz and in some instances make up as much as ten percent of the rock. The sulfides carry a large proportion of the values. Coarse free gold is reported by Thomson and Ballard (10, p. 110)¹ from a sample of ore from the Big Buffalo Mine. Secondarily enriched ores are of minor importance. Those which may have been present in pre-Pleistocene times have been largely removed by glaciation.

SEQUENCE OF MINERALIZATION

Polished surfaces of ore collected in the St. Louis Tunnel were examined and the sequence of mineralization was found to be as follows:

1. Deposition of massive quartz and pyrite.
2. Deformation and fracturing of quartz and pyrite.
3. Introduction of quartz, sphalerite, chalcopyrite and galena. The latter continued to be deposited for a short time after the cessation of deposition of sphalerite and chalcopyrite.
4. Deformation.

The pyrite and quartz, it is believed, are essentially contemporaneous. The pyrite is usually in well developed crystals scattered irregularly throughout the rock and is not found along re-healed fractures, as would be expected if it were deposited distinctly later than the quartz.

Following the primary deposition of quartz and pyrite came a period of deformation, which brought about an intimate fracturing of the quartz and pyrite. The photomicrographs (Fig. 8 and Fig. 9) show

¹ This paper had not appeared at the time the writer began his field work, and his observations were made without knowledge of the information contained in it.

this feature clearly. Quartz, sphalerite, galena and chalcopyrite were deposited in the fractures, and there was, in addition, some replacement of the older minerals outward from the fissures. Figures 8, 9 and 10 show the veining of the shattered pyrite and quartz by sphalerite, galena, chalcopyrite and a second generation of quartz. Sphalerite, chalcopyrite and galena are all essentially contemporaneous. They frequently form intergrowths with irregular curved contacts. Chalcopyrite



FIG 8.—Photomicrograph of polished surface of ore from the St Louis tunnel
Showing crushed fragments of pyrite (py) and veinlets of quartz (q) and galena (ga)
filling spaces between the pyrite fragments. $\times 25$.

occurs typically as small specks enclosed in sphalerite. Galena apparently continued to be deposited for a short time after chalcopyrite and sphalerite deposition had ceased, since there are galena veinlets cutting sphalerite (Fig. 10).

Deformation continued even after the deposition of galena. In the polished surfaces, single crystals of galena are sometimes extensively pitted. The pits are triangular in shape with sharp angles and are formed by the breaking out of cleavage fragments. In all cases the pits are rudely aligned. The lines are frequently curved (Fig. 11) and this is taken as indicating deformation after the deposition of galena.

TIME AND TEMPERATURE OF VEIN FORMATION

In the area occupied by the vein system the granite and schist are cut by numerous pegmatite dikes. Several large ones striking nearly parallel to the quartz veins outcrop in a strip extending from the Dewey claim southward toward Deer Lake. None of the pegmatite dikes pass longitudinally into quartz veins at the surface. On the St. Louis and

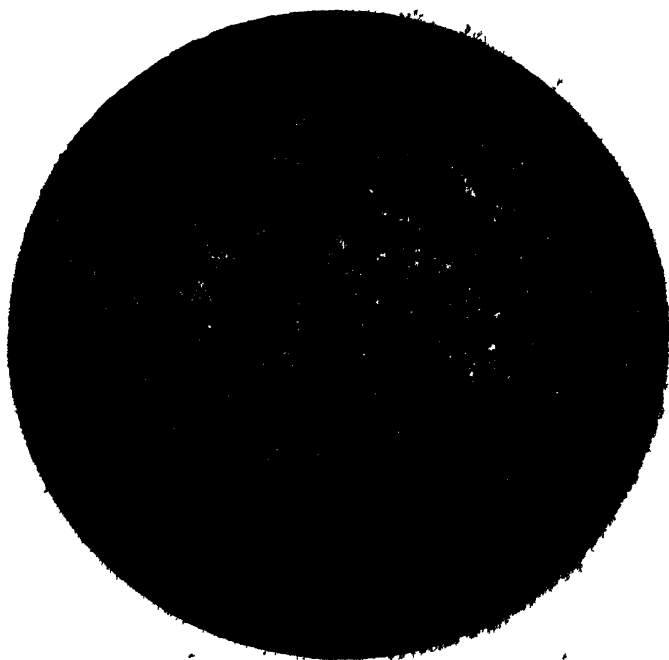


FIG. 9.—*Photomicrograph of polished surface of ore from the St. Louis tunnel*
Showing crushed fragments of pyrite (py) and veinlets of quartz (q) and galena (ga)
filling spaces between the pyrite fragments. $\times 25$.

San Francisco claim the vein cuts a large pegmatite dike at a small angle. There has been very little alteration of the schist in contact with the vein. Microscopic examination of a schist specimen taken a few inches from the vein reveals comparatively little alteration other than slight chloritization of the biotite. Where the schist is in contact with the dike, it has been extensively altered for twenty feet and changed to a light-colored, fine-grained rock with parallel bands of

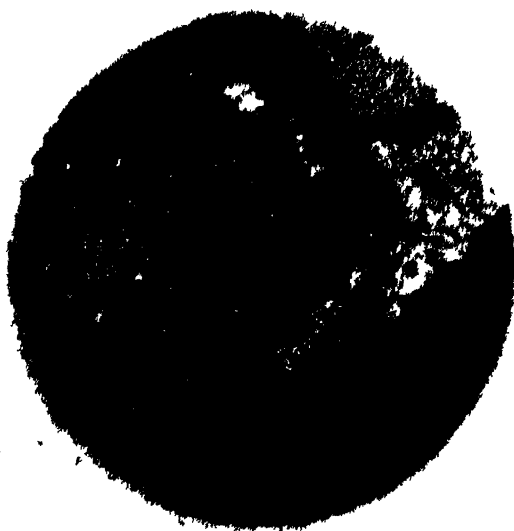


FIG. 10.—Photomicrograph of polished surface of ore from the St. Louis tunnel
Showing intergrowths of sphalerite (sp) and chalcocite (ch) and veinlets of galena (ga) penetrating sphalerite.
× 25.

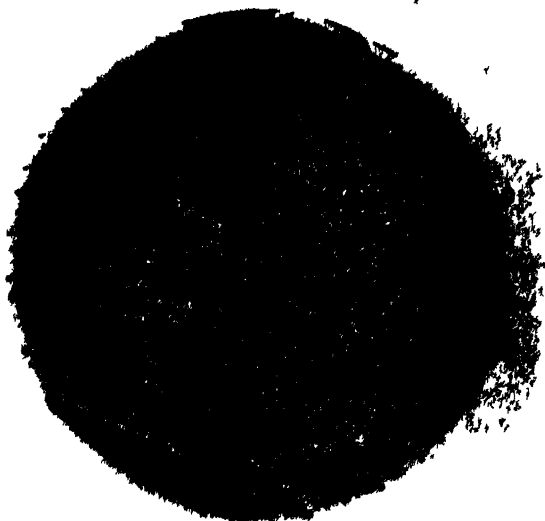


FIG. 11.—Photomicrograph of polished surface of galena from the St. Louis tunnel
Showing the curved lines of pits. (See description in text)
× 25.

dark minerals marking the former planes of schistosity. Under the microscope the characteristic quartz mosaic of the schist is still visible, but there has been extensive recrystallization and introduction of material from the pegmatite, giving feldspar, garnet, apatite, titanite and tremolite.

The fact that the quartz vein cuts a pegmatite dike, the contrast in the respective alteration effects of the vein and pegmatite dike, and the association of vein minerals characteristic of mesothermal ore deposits all combine to indicate that the St. Louis and San Francisco vein, at least, was formed at a stage of consolidation of the batholith distinctly later than that of pegmatite intrusion. In other cases the relation of the veins to the large pegmatite dikes is not so clear. None of the other veins, however, were seen to pass longitudinally into pegmatite dikes and in some places they cut granite of coarse pegmatitic type. Along all of the veins the predominant types of alteration are sericitization and silicification. This is in marked contrast to the contact metamorphic effects produced by the granite, pegmatite and aplite dikes with which are associated such minerals as the feldspars, garnet, apatite, tourmaline, titanite and tremolite, all of which are characteristic of high temperature. The veins were formed at a temperature much lower than the pegmatites, probably below the critical temperature of water.

VALUE OF THE DISTRICT

At present none of the properties of the district are producing. The principal reasons for closing operations were: (1) the expense of transportation, (2) the scarcity of timber in the immediate vicinity, (3) the loss in treatment of the ores by amalgamation only and (4) the expense of shaft mining. The solution of the first of these difficulties by the construction of a railroad or a road suitable for heavy trucking would overcome the second and third. The surrounding country at lower altitudes is heavily forested and timber could be obtained within a few miles. If extensive development were undertaken, the expense of shaft mining could be overcome by running in tunnels from the deep canyons converging toward the divide on which the veins outcrop.

When the writer visited the camp most of the deeper workings were closed by caving or burning of timbers by forest fires. Consequently it was impossible to obtain fresh samples except from a few properties. All of these were from near the surface. The district was visited in 1917 by a United States Bureau of Mines party. This party reported (13, p. 44) values running from \$8 to \$15 per ton and tailings carry-

ing about \$2.50 per ton. Eight feet is indicated in the report as the average width of the veins. This figure is considerably larger than the estimate (four feet) made by the writer from the surface exposures, but this discrepancy is to be expected, since the Bureau of Mines party apparently had access to some of the deeper workings. The length of the veins (see Fig. 7) is another feature which makes a very favorable showing for the camp.

A question of major importance is that of the continuation of values in depth. Varley, Wright, Soper and Livingston (13, p. 44) state that the Jumbo Mine has been developed to a depth of 800 feet and very little change in the tenor of the ore has been noted. Other information on observed changes in value content is lacking, but certain features of the veins themselves indicate that there is probably no considerable change in character downward. Although the veins are in many places in contact with the granite, the veins are of the medium temperature type and were formed considerably later than the stage of pegmatite intrusion. It seems logical to conclude that, at the time of vein deposition, the zone in which the veins now outcrop had cooled far below the temperature of consolidation of the batholith, while the source from which the mineralizing solutions came was deep within the granite. It is to be expected, then, that the veins extend downward toward this source and that they have features at a considerable depth similar to those of the veins at the surface.

WAR EAGLE AND BLUE JAY PROPERTIES

In the southeast corner of the district examined are the War Eagle and Blue Jay properties, both of which are deeper within the granite than the vein group of Buffalo Hump. A large block of quartzite within the granite at an altitude of 800 feet above the War Eagle lower tunnel and half a mile to the northwest may give some indication as to the depth of the ore deposit below the roof of the batholith. Thomson and Ballard (10, p. 76) give 2000 feet as a minimum, but this figure is probably too large. It is quite certain that the depth of the ore body below the roof was greater than 800 feet, but the quartzite block shows that the roof was not far above.

BLUE JAY PROSPECT

At the Blue Jay prospect the quartz occurs at intervals in brecciated material between nearly vertical, slickensided walls striking N. 73° W. The quartz appears to be in vertical chimneys, but sufficient work has

not been done to justify the conclusion that this is always true. A fine-grained basalt dike cuts the crushed material in the main tunnel. It has been disturbed, but the movement has not been extensive. The deformation of the dike is due to a minor movement along the fault at some time after the main brecciation. A specimen of altered basalt was collected for microscopic examination. It shows no silicification, but is extensively carbonated. The carbonate is in coarse veinlets and there is no microscopic veining and impregnation of the rock, as is frequently the case when carbonation is carried on by hydrothermal waters. It is believed that the alteration of the dike was accomplished by meteoric and not by magmatic waters. The dike cuts the vein at a place where the brecciated material is not silicified. Consequently the lack of silicification of the basalt has no bearing on the time relations of dike intrusion and ore deposition.

The Blue Jay ore consists of quartz gangue with sphalerite, galena and chalcopryite in veinlets. Its general history is similar to that of the ore from the St. Louis and from the War Eagle to be described below; i. e., (1) deposition of gangue, (2) fracturing, (3) introduction of sphalerite, galena and chalcopryite along fractures.

WAR EAGLE MINE

The War Eagle deposit is a replacement of granite in a crush zone. Quartz and pyrite were the first constituents of the mineralization. After a second fracturing, quartz, sphalerite, chalcopryite and galena were introduced and are found as veinlets cutting the older generation of quartz and pyrite. Sphalerite and galena are contemporaneous in part and are found in intimate intergrowth. Galena and chalcopryite continued to be deposited for a short time after sphalerite, since veinlets of intergrown galena and chalcopryite cut sphalerite. Thomson and Ballard (10, pp. 79-80) report essentially the same history. C. F. Tolman (11) working with material collected from a different locality in the same ore shoot, found slightly different relations. Tetrahedrite is present and was found to be essentially contemporaneous with sphalerite. Tolman says that there is a pronounced gap between the deposition of galena and the other sulfides, but of shorter duration than that between them and pyrite. He also mentions inclusions in the galena of a mineral which is probably a gold-silver telluride and inclusions in galena of argentite as a primary mineral and not as a product of downward secondary enrichment.

CONCLUSION

The quartz veins of the Buffalo Hump group, the War Eagle and the Blue Jay are of the "fissure vein" type. The foregoing statement is not to be construed as meaning that the veins were formed in open cavities. These may have existed at some points, but the field observations seem to indicate that the ore was deposited by waters carrying on replacement along lines of weakness produced by faulting. At the War Eagle and Blue Jay the close connection between brecciation and localization of vein material is very evident. Underground in the Del Rio Mine the irregular fragments of partially replaced granite at the margins of the ore lead to the same conclusion. The reported absence of a well-defined hanging wall in the underground workings of the Concord Mine may have a similar significance.

The observation that the quartz veins cut pegmatites and the apparent absence of veins passing longitudinally into pegmatite dikes point to the lack of any genetic connection between them except their common derivation from the batholith. The strong contrast in respective alteration effects of the veins and pegmatites and the assemblage of vein minerals characteristic of mesothermal deposits indicate that the veins were formed in a late stage of consolidation of the batholith when the high temperature zone was far below the present surface on which the veins outcrop. It is extremely probable, therefore, that the veins continue downward for a considerable distance without any essential change in character. It is not believed that the quartz veins are "veindikes." The successive steps of deformation and mineralization lead to the conception of ore genesis as a process of deposition of mineral material by magmatic waters in zones of weakness along which there was more or less continuous movement with alternating periods of comparative activity and quiescence.

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THE SCENERY OF MT. DESERT ISLAND:
ITS ORIGIN AND DEVELOPMENT

BY
ERWIN J RAISZ



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CHROMOSOME IRREGULARITIES IN RELATION TO STERILITY IN *HEMEROCALLIS FULVA* CLON EUROPA*

A. B. STOUT
N. Y. Botanical Garden

AND

TORASABURO SUSA
Aomori Agricultural Experiment
Station, Japan

CONTENTS

	Page
Introduction	2
Chromosome behavior in somatic divisions.....	3
The basic or normal number of chromosomes.....	3
Irregularities in the number of chromosomes in somatic cells.....	4
Chromosome and nuclear behavior during sporogenesis.....	5
Synapsis	5
The normal number of chromosomes in diakinesis.....	5
Irregularities in the number of chromatin units in diakinesis and in the first meiotic division	6
Normal stages in sporogenesis.....	8
The various types of irregularities.....	8
Irregularities in the distribution of chromatin in the first division	9
Irregularities in the formation of cell plates in the first meiotic division	9
Irregularities in the distribution of chromatin during the sec- ond division of meiosis	9
Irregularities in the shape of chromatin masses.....	10
The stretching of chromatin material between nuclei.....	11
The microspores and macrospores.....	11
The number of microspores.....	11
Variations in the size of the microspores.....	12
The nuclei and the chromosome number in microspores.....	13
The viability of the pollen.....	13
The abortion of macrospores.....	13
Summary and discussion.....	14
Summary of the chromosome and nuclear behavior in the Europa clon	14
The chromosome number for the Europa clon.....	16
Increase in the number of chromatin units.....	18
Types of sterility involving abortion of spores.....	20
The inherent and hereditary nature of spore abortion.....	24
The immediate causes of spore abortion.....	25
Bibliography	27

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INTRODUCTION

Plants of the single-flowered fulvous daylily, commonly and widely cultivated as *Heemerocallis fulva*, are decidedly sterile by an abortion of the majority of both the microspores and the macrospores. It is the cytological study of the nuclear phenomena associated with this sexual impotence that is to be reported in this paper, and this study has become chiefly an analysis of the behavior of the chromosomes and of their multiplication not only in meiotic divisions but in somatic mitosis as well.

In considering the significance of the cytological data from these plants, it should be remembered that all the plants of this particular type of daylily are propagated, and evidently always have been propagated, only by vegetative means. This is necessary because for them there is a complete incompatibility between such of the germ cells as are functional. Evidently the many plants of this one type of daylily, which are now growing rather widely throughout the world either as a cultivated plant or as a frequent escape, constitute a single clon. The various cytological studies that have thus far been reported for plants named as *Heemerocallis fulva* involve, it appears, only plants of this commonly cultivated single-flowered clon and hence relate to the various branches of one seedling plant.

Two double-flowered types of the fulvous daylily, described as var. *Kwanso* and var. *flore-pleno*, that are obviously very closely related to the single-flowered clon, are also in cultivation. Single-flowered plants presumably belonging to this same species are to be found growing wild in the Orient. Some of these, such as the *H. fulva* clon *Maculata* have more recently been introduced into garden culture. During the last few years a considerable number of plants of the wild stocks of this species have been obtained directly from Japan and China and are being grown at The New York Botanical Garden for study and for use in breeding (Stout, 1925). Thus far all such plants have been observed to differ in some particular from plants of the commonly cultivated single-flowered clon that is known as *H. fulva*, although in some of these plants the differences are slight. The plants of these wild stocks also differ among themselves. Thus it appears that the species to which this clon is most closely related and in which it is evidently to be included comprises several varieties or races.

The plants of the type commonly cultivated and widely known as *H. fulva* are, so far as we are able to determine, uniform to an unusual degree. Living plants of this type obtained from such widely separated

localities as Italy, France, Holland, Sweden, England and various sections in the United States have been grown together at The New York Botanical Garden and have been carefully compared. These plants are all indistinguishable. The studies to be reported in this paper relate primarily to this vegetatively propagated and widely cultivated clon of the single-flowered fulvous daylily. These plants will be referred to as the "*H. fulva* clon Europa."

At least twenty different papers have already been published which deal with various aspects of the cytology of plants of this clon Europa. In several of these papers it is reported that in these plants frequently more than four pollen grains are formed from one pollen mother cell. This fact was reported for this clon as early as 1882 by both Tangl and Strasburger. Tangl (1882) concluded that these extra pollen grains arise after the reduction divisions have been completed by the further divisions of certain of the cells of the quartet. Strasburger, later in the same year (1882), showed that irregularities appear in the first meiotic division by the lagging of chromosomes, which then form small accessory nuclei. Further and more extended studies were made by Juel (1897), who found irregularities in the distribution of the chromosomes and in the formation of the nuclei both in the first and the second meiotic divisions.

In general these papers present an excellent account of the irregularities that result in the unequal distribution of chromosomes, in the lagging of chromosomes and in the formation of micro pollen grains. These earlier authors, however, did not settle the question as to what the normal and basic number of chromosomes is for plants of this clon, and what is the range and the method of the variations in number beyond and below that which is normal.

Our studies show that the basic diploid chromosome number for plants of the clon Europa is 12, but that the number may increase both in somatic and in meiotic divisions, and that during micro-sporogenesis increases in the number of chromosomes and of chromatin units are combined with irregularities in their distribution, with other abnormalities in nuclear division, and with the erratic organization of nuclei until finally there is an abortion of spores that is almost complete.

CHROMOSOME BEHAVIOR IN SOMATIC DIVISIONS

THE BASIC OR NORMAL NUMBER OF CHROMOSOMES

The normal number of chromosomes in the somatic cells of plants of the Europa clon is 12. During the stages of nuclear division in somatic

cells the chromosomes are long rod-shaped structures very uniform in size, and each is clearly a single chromosome and not a group of two or more chromosomes. In these figures the chromosomes are often rather closely aggregated and more or less intertwined. But whenever the chromosomes are spread out in an *early* stage of the equatorial plate sufficiently to admit of accurate count, the number has been found to be most frequently 12 as shown in Pl. I, Fig. 1. But the chromosomes may, in some cases at least, divide and separate quickly and very completely, so that one can best determine the correct somatic number during the early stages of the equatorial plate (Pl. I, Fig. 1), or later in the anaphases when all the chromosomes have completely divided and the two sets are fully separated (Pl. I, Fig. 2).

IRREGULARITIES IN THE NUMBER OF CHROMOSOMES IN SOMATIC CELLS

For many cells in the embryonic regions of the root tips and of the stems the distribution of the daughter chromosomes during the anaphases is regular, resulting in the passing of 12 chromosomes to each daughter nucleus (Pl. I, Fig. 2). However, cases of unequal distribution involving non-distribution* of certain pairs of daughter chromosomes are to be found which result in daughter nuclei with the numbers 11 and 13, or of 10 and 14. Still greater inequalities of distribution are to be seen. Especially when cells are of asymmetrical shapes, they may divide in such a way that only a few chromosomes pass to one pole. This is shown in Pl. I, Fig. 3, in which there is a normal total of 24 chromosomes in an anaphase stage, but non-distribution is so general that 19 chromosomes are collecting at one pole. Thus in a single mitosis of a somatic cell that had 12 chromosomes, the number of chromosomes which a daughter nucleus may receive may rise to at least as many as 19.

In the division of nuclei which have previously received an increased number of chromosomes, further non-distribution of chromosomes may occur, giving nuclei with varying numbers of chromosomes above the normal of 12, and in some cases the number may rise to more than double the normal diploid number.

* The term "non-distribution" will be used in this paper to designate those cases either in somatic or in meiotic divisions where two daughter chromosomes form and separate by the splitting of a mother chromosome, but are not distributed to different daughter nuclei. The term "non-disjunction" applied by Bridges (1913) will be here employed only for cases where two homologous chromosomes of a pair are not distributed to different daughter nuclei during the meiotic divisions. According to Wilson (1925, p. 872) and to Sharp (1926, p. 400) the term non-disjunction can be applied both to the non-disjunction of homologous chromosomes during meiosis and to the non-distribution of sister chromosomes in somatic divisions, but a distinction as here suggested seems highly desirable.

An extended search has been made in somatic tissues prepared by the paraffin method in the effort to determine for plants of the Europa clon the frequency of nuclei having increased numbers of chromosomes and the range of these numbers. The counts are most easily made in the late stages of the anaphase of mitosis. In some root tips only the normal numbers of 12 and 12 were found. In other root tips of the same plant, cells with increased numbers of chromosomes were observed intermingled with cells that had the normal number. Division figures, such as are shown in Pl. I, Figs. 2 and 4, were noted side by side in a single root tip, but in most cases the large majority of the cells possessed the normal number. The highest number of chromosomes recorded thus far for the division of any somatic cell is 56 (Pl. I, Fig. 5).

Arber (1920) has reported that the somatic cells in certain portions of the flowering axis of plants of *H. fulva* are commonly binucleated or even multinucleated. Such cells have not been observed by us either in the somatic tissues, where mitosis has been especially studied, or in the pollen mother cells, although they have been noted among the tapetal cells.

CHROMOSOME AND NUCLEAR BEHAVIOR DURING SPOROGENESIS

SYNAPSIS

The stages of synapsis have been very carefully studied for various plants of the Europa clon obtained from different localities in Europe and America. In every plant the synapsis of pollen mother cells was very uniformly normal. Disintegration such as is described by Timm (1928, Abb. 1) was not found to a noticeable degree in the nuclei of spore mother cells. Also, in no case were two resting nuclei or two synaptic knots noted in a single spore mother cell. Special study was made of this point, for it is important to know whether the presence of two nuclei in pollen mother cells is a factor in the increase in the number of chromosomes observed in later stages, as is reported to be the case by Karpechenko (1927) for certain hybrids between *Raphanus sativus* and *Brassica oleracea*.

THE NORMAL NUMBER OF CHROMOSOMES IN DIAKINESIS

During diakinesis the total number of individual chromosomes in many of the nuclei is apparently 12, which is in agreement with the normal diploid number in the somatic cells. These may occasionally be arranged

as six bivalents (Pl. I, Fig. 10) but usually there are various numbers of bivalents. The following groupings of chromosomes have been found in this stage: —6 pairs; 5 pairs + 2 single; 4 pairs + 4 single; 3 pairs + 6 single; 2 pairs + 8 single; 1 pair + 10 single; and 12 single, which are all the combinations of bivalents and univalents possible for a total of 12 chromosomes. Nuclei with more than six chromatin masses are frequent in cells that are in the stages of diakinesis and in many cases the number is obviously due to the presence of univalents. Thus in Pl. I, Fig. 7 there are evidently four bivalents and four univalents, making a total of eight chromatin masses involving a total of 12 chromosomes, which is the normal diploid number.

IRREGULARITIES IN THE NUMBER OF CHROMATIN UNITS IN DIAKINESIS AND IN THE FIRST MEIOTIC DIVISION

A study of numerous nuclei in diakinesis and in the early stages of the first meiotic division reveals that many nuclei possess more than 12 masses or units of chromatin. Thus far the highest number of masses observed during diakinesis is 24 (Pl. I, Fig. 9), which was found in an aceto-carmin preparation. In this and in similar preparations many of the masses present are obviously single, but there are also cases of several masses more or less connected. In nuclei at this stage (Pl. I, Fig. 8) certain of the masses present evidently comprise more than the equivalent of two of the smaller masses. Thus the number of chromatin masses present in a nucleus during diakinesis is frequently greater than 12 and there are noticeable irregularities in their relative sizes and shapes.

Possibly the number of chromosomes present in certain pollen mother cells may sometimes be more than 12 due to an irregular distribution in the somatic divisions that precede their formation, such as occurs in the cells of the roots. But such conditions as are shown in Pl. I, Figs. 7, 8 and 9, indicate that there are frequently failures in the reconstruction of chromosomes after synapsis. The evidence is very positive that the breaking up of chromosomes into fragments may and does occur during diakinesis (Pl. I, Figs. 8 and 9). Later, during the early stages of the first meiotic division, fragmentation of chromosomes is also frequent. Thus in Pl. I, Fig. 12 the six bivalents are in the earlier stages of fragmentation and segmentation and in Pl. I, Fig. 16 all the bivalents and univalents are in the process of breaking up into numerous pieces. Later, after the fragments are more or less separated and there is a failure or a delay in the organization of nuclei, the total number of pieces of

chromatin may be as high as 50 or more (Pl. II, Fig. 24) and some of these may be very small.

During the first meiotic division an increase in the number of chromosomes may and often does occur by the division (longitudinal splitting) of univalents, such as regularly occurs in somatic divisions and in the second meiotic division. In the equatorial plate of the first division the univalents are often smaller than the bivalents, even when the univalents are in the process of dividing. This is well shown in Pl. I, Figs. 13 and 14, which are of two pollen mother cells lying side by side in the same anther with the nuclei of both in the equatorial plate of the first division. In Pl. I, Fig. 14 there are 12 univalents and each is dividing. In Pl. I, Fig. 13 there are 5 bivalents and 2 univalents. A slightly later stage is shown in Pl. II, Fig. 17, with 12 chromatin masses passing to each pole. Most of these appear to be double due to the beginning of a second splitting. Thus from 12 univalents it is possible that a total of 48 chromosomes may develop by two successive divisions. With complete pairing and no fragmentation there is usually a reduction division, although irregular distribution and non-disjunction may follow. With increasing numbers of univalents the first division becomes more and more like that of a somatic cell. When all 12 chromosomes are univalents and there is division of each in the first division (Pl. I, Fig. 14), a reduction of chromosomes is omitted and the division is identical with that in somatic mitosis. Certain of the figures given by Juel (1897) indicate that he had before him such a condition. It seems probable that it was from observing such figures that Strasburger (1900) was led to decide that the normal diploid number of chromosomes for plants of *H. fulva* (the clon Europa) is 24.

To summarize: during diakinesis and the first meiotic division marked irregularities frequently develop in respect to the number of chromatin units. Through the division of univalents the number may range from the normal 12 to as many as 24. When there is also fragmentation, the number of chromatin pieces may be greater. As a result the numbers in the metaphases of the first division are very often more than 12; they rather frequently rise to 24, and a total of more than 30 is to be found. Further chromosome division and fragmentation in the second meiotic division may again increase the number of chromatin units, although the later splitting of chromosome units is very often not completed, at least when the number has already been increased and especially when the increase has been by the splitting of univalents.

NORMAL STAGES IN SPOROGENESIS

Stages of sporogenesis that are normal in some one particular are frequently to be observed. In Pl. II, Fig. 19 there has been disjunction of all the 6 pairs of chromosomes but 1 chromosome is lagging. In Pl. III, Fig. 32 the shape of the chromosomes is normal and they are in four groups but the distribution has not been equal. In Pl. III, Fig. 34 are shown four sister nuclei of nearly equal size, and each nucleus evidently contains 6 chromosomes that are now greatly increased in size and especially in length, but at least some of the chromosomes may be abnormal, for there are present some of the enlarged X-shaped chromosomes that will be discussed later. A pollen grain with its primary nucleus in mitosis with 6 rod-shaped chromosomes present is shown in Pl. III, Fig. 36, the number being half of the normal number of 12 which is found in the somatic cells of the plant. That the number of chromosomes at this stage may sometimes be greater than 6 is shown in Pl. III, Fig. 37. Thus certain normal conditions are to be noted along with numerous abnormalities at all stages in the processes of sporogenesis.

A development that produces four pollen grains in a tetrad group from one pollen mother cell is, of course, to be considered normal in respect to the number of spores formed. A functional pollen grain is one that will act in fertilization and a fully normal spore is, we may consider, one in which each nucleus possesses 6 chromosomes (Pl. III, Fig. 36). It may, however, be conceived that pollen grains which carry more or less than a complement of 6 chromosomes may function in fertilization. The hybrids obtained with the Europa clon are being studied for evidence on this point.

THE VARIOUS TYPES OF IRREGULARITIES

We may further summarize the irregularities that occur during sporogenesis in plants of the Europa clon as follows: (a) the increase in the number of chromatin units as already described, (b) the irregular distribution of the chromatin units, (c) the development of anomalous shapes in chromosomes, (d) the irregular and abnormal organization of the daughter nuclei, (e) the omission of one of the reduction divisions, (f) the formation of abnormal numbers of microspores with the abortion of many of them and (g) a failure in the proper divisions of the primary or the generative cells in certain of the pollen grains.

IRREGULARITIES IN THE DISTRIBUTION OF CHROMATIN IN THE FIRST DIVISION

Perhaps the simplest phenomenon in the irregular distribution of chromatin is the lagging of a single chromosome in the first meiotic division (Pl. II, Figs. 19 and 20) or the isolation of a pair that has not disjoined. As already stated, this may occur when the number is normal (12 diploid) and there has been complete pairing. A small accessory nucleus may then be formed, as was described and figured by Strasburger (1882). There may be more than one lagging or stray unit. The distribution in the first division may give three or more groups with various numbers in each. A case of three groups with four chromosomes (some already split or fragmenting) in each is shown in Pl. II, Fig. 21. With an increase in the number of chromatin units and of chromosomes during the early metaphases the distribution that follows becomes increasingly irregular.

IRREGULARITIES IN THE FORMATION OF CELL PLATES IN THE FIRST MEIOTIC DIVISION

Cell plates may or may not be formed at the close of the first division. When a plate is fully developed, it results in two cells either with the nuclei organized, permanently or merely for a time, or with the chromatin units scattered. There appear, however, to be few cases where only two spores are formed from one pollen mother cell, hence such conditions as are shown in Pl. II, Fig. 27 are usually followed by the division of at least one of the two cells. Where three or more nuclei are formed after the first division and these become fully separated by cell plates, further division evidently does not occur at least in the case of most of the cells. Most instances of three microspores in a group and some of the instances of four spores of irregular size are the products of only one regular division. In many cases the chromosomes pass on into the second division without the formation or the persistence of definite cell plates (Pl. II, Fig. 30 and Pl. III, Fig. 31). When the number of chromatin units is large, as after fragmentation, the units may lie scattered throughout the cytoplasm (Pl. II, Fig. 24) and the organization of the nuclei is delayed and irregular, the entire group passing on into the second division without the formation of a definite nucleus.

IRREGULARITIES IN THE DISTRIBUTION OF CHROMATIN DURING THE SECOND DIVISION OF MEIOSIS

In the second division or in the final stages preceding the formation of the nuclei, the distribution of the chromosomes is most often irregular

even though the shape of the chromosomes is normal and their number is normal or nearly so. Pl. III, Fig. 31 shows a distribution into five groups of 3, 4, 6, 6 and 7 chromosomes that are all quite normal as to shape, the total being 26 or only 2 more than the normal for the four microspores that normally develop. In Pl. II, Fig. 30 four groups composed of 12, 16, 17 and 18 chromosomes are to be seen, and nearly all the chromosomes are of the normal rodlike form. Here the number of microspores that are forming is normal, but the numbers of chromosomes are increased to a total of 63 instead of the normal total of 24 for all the members of a quartet. In such cases there were either fragmentations with divisions of chromatin units in both the first and the second meiosis or the number of chromosomes that entered synapsis was greater than 12.

IRREGULARITIES IN THE SHAPE OF CHROMATIN MASSES

The abnormal shapes that chromatin masses or units very frequently take and retain begin to develop in the late stages of the first division (Pl. II, Fig. 18) and become well developed in the equatorial plates of the second division (Pl. II, Fig. 25). In the latter stage irregular and X-shaped chromatin masses are commonly seen. In the majority of cases each of these appears to be composed of two daughter chromosomes that have remained attached at the middle and have failed to complete a separation. Among the groups of such structures some may be found with the two rods of the X separating quite as do daughter chromosomes while others are much lobed and very irregular in shape. To count these structures as double or as two daughters would in many cases give a total of more than 60 instead of the normal number of 24 for all nuclei of a completed second division.

When these X-shaped chromatin bodies are assembled into two groups after the anaphase of the first division, they may appear as represented in Pl. II, Fig. 25. In this particular figure there are 17 in one group and 13 in the other. At this stage the number for the two groups frequently varies around 30. It was a figure similar to this that led Belling (1925) to believe that there are 33 chromosomes, or three sets of 11, in the somatic cells of plants of the *Europa* Daylily. Belling, however, made no studies of the somatic divisions.

It is perhaps a significant fact that the X-shaped and apparently double chromosomes have not been found when the total number for the second division is nearly normal—that is when there are but 6 splitting chromosomes for each of the two equatorial plates of the second

division and 6, or close to that number, for each of four spores when that number develops from a single pollen mother cell.

The fate of these X-shaped chromosomes or cohering pairs of daughter chromosomes is a matter of interest. That they may remain in this condition and pass into the primary nucleus of spores is indicated in Figs. 33 and 35. But thus far in the mitosis of the primary nucleus of microspores only rod-shaped chromosomes have been noted (Pl. III, Figs. 36 and 37), which may indicate that nuclei receiving the X-shaped chromosomes do not reach this more advanced stage of development, or that the two pairs of the X become separated, or that they combine to make a single rod. The shapes of chromatin masses may be still more abnormal in that they may become much lobed or even almost amoeboid in shape (Pl. II, Fig. 24).

THE STRETCHING OF CHROMATIN MATERIAL BETWEEN NUCLEI

The stretching or stringing out of a single chromatin unit, as described by Juel (1897), is frequently to be seen during both the first and the second division, and this may continue or persist even after the reorganization of the nuclei. In Pl. II, Fig. 22, which is a telophase of the first meiotic division, one chromatin unit is stretched between two daughter nuclei with a part in each. Quite the same condition is shown in Pl. III, Fig. 33 after the nuclei resulting from the second division are fully formed. Evidently the two ends of a single chromosome may be included in two different nuclei, or two daughter chromosomes which have remained attached to each other are thus distributed.

THE MICROSPORES AND MACROSPORES

THE NUMBER OF MICROSPORES

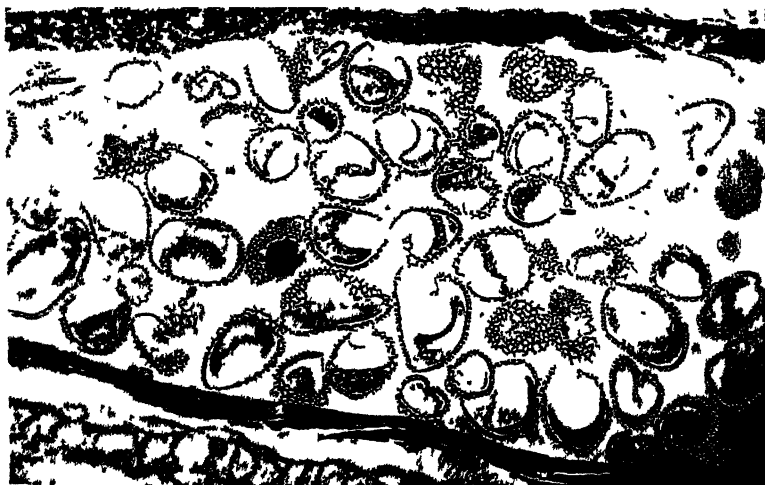
The number of microspores that may develop from a single pollen mother cell has been especially studied in fresh material by using the aceto-carmin method. In only one case has but one large cell been found to be derived from a pollen mother cell. In the cytological preparations of meiosis the chromatin masses frequently lie scattered within one cell with little indication of spindle fibres, but evidently divisions which give two or more spores occur sooner or later. The number of spores formed from a single pollen mother cell and their relative sizes, with the frequency for each in the 624 cases counted, are as follows:—

1 large spore,	1 case
2 large spores nearly equal in size,	3 cases
3 spores of irregular sizes,	18 cases
4 spores of uniform sizes,	119 cases
4 spores of irregular sizes,	174 cases
5 spores of irregular sizes,	198 cases
6 spores of irregular sizes,	84 cases
7 spores of irregular sizes.	20 cases
8 spores of irregular sizes,	6 cases
9 spores of irregular sizes,	1 case

From such a survey it appears that the normal number of four spores is formed from nearly one half of all pollen mother cells, but that in more than half of these cases the spores are irregular in size. In about one-fifth of all the cases four spores of nearly uniform size are formed. The omission of any division, which gives but one spore from a pollen mother cell, occurs rarely.

VARIATIONS IN THE SIZE OF THE MICROSPORES

The microspores have been especially studied in cytological preparations made from anthers that were about to dehisce. There is consider-



Photomicrograph of pollen grains in the anther shortly before anthesis, showing the large proportion of undersized and shrivelled microspores.

able variation in the size of the grains with all gradations between the extremes. The mature dry grains are ovoid in shape with a conspicuous

fold or crease along one side in the long axis. In the sections (see text figure) certain grains are cut in their short axis and hence appear out of proportion to the grains that lie with the long axis in view. A considerable number of the grains are undersized, shrivelled and of irregular shapes. Nearly all of the cells have the exine with its reticulations developed to some degree, and relatively few of these spores are entirely lacking in protoplasmic contents.

THE NUCLEI AND THE CHROMOSOME NUMBER IN MICROSPORES

In many of the microspores, at the time anthers are about to dehisce, there is a single nucleus, which is in the resting condition and which possibly does not develop further. But division figures for the formation of the vegetative and the generative cells are to be found. In some of these 6 chromosomes are present (Pl. III, Fig. 36); in others more than 6 are to be seen; but thus far the largest number noted has been 18 (Pl. III, Fig. 37). In all these divisions thus far observed only rod-shaped chromosomes have been found. The two-celled stage of the microspore following the division of the primary nucleus is rather frequently seen, with the smaller generative cell lying to one side of and entirely outside of the vegetative cell. In many such microspores further development evidently does not take place.

THE VIABILITY OF THE POLLEN

Many tests for the germination of pollen have been made over a period of ten years and involving many plants of the Europa clon obtained from various widely separated countries. There is excellent germination of about 3% of the pollen grains on a medium of 1% agar with 10% or 15% cane sugar. In no test has more than 5% of all the microspores germinated and only well-formed grains of good size have germinated. The viable pollen grains make fine long tubes and, as pollen is abundant in the anthers, it would seem that sufficient viable pollen is produced to yield seed freely when there is a compatible relation in fertilization.

THE ABORTION OF MACROSPORES

The abortion of the macrospores has not been studied in detail by cytological methods, but the behavior of plants of the Europa clon in respect to seed-setting indicates that abortion is quite the same in degree for macrospores as for microspores. To all self-pollinations there is complete self-incompatibility; the ovaries make no start toward de-

velopment and there is prompt abscission. In more compatible cross-pollinations the pollen tubes penetrate to the ovules and the ovaries enlarge and develop for some time. Many of these young capsules are entirely empty; some contain only one seed each but these capsules usually shrivel and fall before they are ripe. Occasionally a capsule will mature and yield ripe viable seeds but thus far the greatest number of seeds obtained from a single capsule is 5 (Stout, 1926). The total number of seeds which a mature capsule of the size typical of the Europa clon should be able to yield is perhaps at least 25. As many as 40 seeds have been obtained from a single capsule of other species. It would seem that in the case of the Europa clon only a few ovules of an ovary are able to function and that even with compatible fertilization these do not usually furnish sufficient stimulation to insure development and to check the ready and early abscission of ovaries characteristic of this clon. The inability to produce more than a very few seeds in a capsule is evidence that the proportion of functional ovules is about the same as the proportion of functional pollen grains.

SUMMARY AND DISCUSSION

SUMMARY OF THE CHROMOSOME AND NUCLEAR BEHAVIOR IN THE EUROPA CLON

The abnormalities that develop during somatic mitosis and during meiosis in plants of the Europa clon are of three main classes:—(1) increase in the number of the chromatin units, (2) unequal and irregular distribution (non-disjunction and non-distribution) of the chromatin units and (3) irregularities in the organization of the nuclei concerned in the processes of meiosis and resulting from them. Due to the abnormalities that develop during sporogenesis, the abortion of spores is almost complete.

In the somatic cells of the root tips a nuclear organization of 12 chromosomes is maintained in the majority of the cells. But non-distribution of chromosomes frequently occurs giving in the anaphases groups of 11 and 13, or of 10 and 14. A non-distribution as great as 19 and 5 (Pl. I, Fig. 3) has been observed. Thus certain nuclei in the root tips receive more than the normal number of 12 chromosomes through non-distribution, and not merely by fragmentation as reported by Hance (1918) for *Oenothera scintillans*. When the number of chromatin units rises to 26 and 30 (Pl. I, Fig. 5) the increase may be brought about by non-distribution, or by fragmentation, or by a combination of both.

When there are such high numbers, some of the units appear to be somewhat shorter than is usual (compare Pl. I, Figs. 2 and 3 with 4 and 5), but this is the only evidence which suggests that segmentation has occurred in somatic divisions. There is definite evidence that the number of entire chromosomes may increase to at least 19 by non-distribution. It seems reasonable to consider that the numbers can increase further by non-distribution to as many as 30, which is the highest number thus far observed in a daughter nucleus in a somatic division (Pl. I, Fig. 5).

No evidence has been found of a completely arrested somatic division in which two sets of daughter chromosomes combine in one nucleus to give a double number, as described by Nemec (1903, 1904) for the somatic cells of root tips treated with solutions of chloral hydrate. In the root tips of the Europa clone the increases in the number of chromosomes arise primarily in non-distribution during the course of the formation of two nuclei.

Thus far no direct and convincing evidence has been obtained which shows that in plants of the Europa clone any of the pollen mother cells receive more than 12 chromosomes. But following an apparently normal synapsis, irregularities in the size, shape and number of chromatin masses are very frequent. Part of this is due to non-pairing, in which varying numbers of univalents are present with the limit of 12 when the chromosomes are all intact and are in normal number. But the number of chromatin units rises above 12 by (1) the failure of chromosomes to develop fully during the early stages of diakinesis or preceding these stages, (2) by fragmentation during diakinesis and in the prophases and the metaphases of the first mitosis, (3) by the omission of pairing and by the splitting of chromosomes in the first meiotic division until, in the extreme, this division becomes the same as a somatic mitosis and (4) by a second splitting in the second division. Thus the normal number of 24 chromosomes for the completed second meiotic division may be increased to at least 60, although in the cases of the highest numbers (Pl. II, Figs. 24 and 30) some of the units may represent fragments of chromosomes.

The number of chromosomes or of chromatin units which nuclei receive in sporogenesis depends in part on variations in the division and multiplication of chromosomes but also on irregularities in their distribution and in the number of nuclei that are formed.

The distribution of the chromatin units is frequently unequal and erratic in both the first and the second divisions of meiosis involving non-disjunction and non-distribution, both when there is the normal

number of chromosomes and when the number is abnormal. The formation of central spindle fibres, of cell plates and of nuclei may also be abnormal in various respects. From one to as many as nine spores may be formed from one pollen mother cell, always, however, with the presence of the phragmaplasts. The number of chromatin elements that enter the microspores varies greatly. Finally, many of the pollen grains are undersized and the poorly developed micro pollen grains regularly contain subnormal numbers of chromosomes. The percentage of viability in germination tests is always low. Tests by cross-pollination indicate that only a small proportion of the ovules are able to function in the fertilizations that give rise to embryos. There is a very decided abortion of both microspores and macrospores that is persistent and very uniform for all plants of this widely cultivated clon.

THE CHROMOSOME NUMBER FOR THE EUROPA CLON

Statements as to the number of chromosomes present in the cells of plants of the Europa clon have been made by several investigators. In his paper of 1882 (p. 496) Strasburger states "Die Zahl der Doppel-elemente in der Kernplatte ist annähernd 12." Evidently this statement refers to the number of paired chromosomes and according to this the somatic or diploid number would be 24. But one of his figures (his Fig. 62) shows only 6 chromatin masses that are evidently bivalents in the equatorial plate of the first meiotic division. Another figure (his Fig. 61) shows 10 masses in diakinesis, which we may now perhaps interpret as including 2 bivalents and 8 univalents. He evidently saw cases where the 12 univalents were all dividing in the first division and considered that this was evidence that the number of paired chromosomes in the reduction divisions is 12. In the material of *H. fulva* studied for his later paper (1900) Strasburger evidently observed many irregularities in the number of chromatin units, which he seems to attribute largely to poor fixation. Thus in his Fig. 65, which is an equatorial plate of the second division, there are 13 masses which appear to be in the early stages of fragmentation. In his Fig. 66, which is one of the groups of the anaphase of the second division, there are 10 split chromosomes, of which several are X-shaped.

Juel (1897) makes no definite statement regarding the number of chromosomes present in plants of *H. fulva*. But his figures reveal various numbers. In the early stages of the first division (his Fig. 2) he shows as many as 10 masses, and in the metaphase and anaphase of this division he presents (his Fig. 6) as many as a total of 24, quite as shown

in our Pl. II, Fig. 17. Juel's Fig. 14 is of one of the two plates of the second division and this one indicates 18 X-shaped or double chromosomes, quite as in one of the groups in our Pl. II, Fig. 25. Juel says in the explanation of this figure that the number of chromosomes is at least 18.

The normal number of 6 bivalents or of bivalents and univalents to the total of 12 univalents seems to be approximated in various of the figures drawn by Strasburger and by Juel, but in other of their figures numbers higher than the normal are to be noted, quite as they are found in our material.

Recently Belling (1925) published a drawing (his Fig. 10) of the metaphase of the first division with 11 chromatin masses, many of which are split and all of which are evidently in stages of fragmentation. He also shows in a late anaphase of a first division or possibly in the prophase of the second division, two groups of 18 and 15 split or X-shaped chromosomes quite similar to the cases which we show in Pl. II, Fig. 25. Belling concludes that a plant of *H. fulva* is a triploid with 33 chromosomes in the somatic cells, but he notes that it must be an irregular triploid with varying numbers of trivalents, bivalents and univalents in the first metaphase. His study did not involve examination of the somatic cells.

Tischler (1927) records the haploid number of chromosomes for plants of *H. fulva* as 16 and cites as the authority a not yet published manuscript from S. Nawaschin.

Schürhoff (1926, p. 461) reviews various of these conflicting statements regarding the chromosome number in *H. fulva* and concludes with the statement "Ich prüfte daher die Chromosomenzahl nach und fand 24 als haploide Chromosomenzahl."

Timm (1928) reports that the haploid number of chromosomes in pollen mother cells of certain plants of *H. fulva* is 12 and he shows (his Abb. 2) an equatorial plate of the first reduction division with 12 chromatin masses, which he considers to be bivalents. He does not report studies of the somatic cells of *H. fulva*, but he states that cells in the root tips of *H. citrina* possess 24 chromosomes. This we do not confirm. Four different strains of *H. citrina* are being grown at The New York Botanical Garden. Sections of the root tips of two of these strains have been studied and in all cases the sections show 12 chromosomes. Since the publication of the paper by Timm the prepared slides of these root tips were carefully re-examined * and the count of 12 fully verified.

* This study was made by Miss Clyde Chandler, technical assistant of The New York Botanical Garden.

Thus the numbers reported for the diploid or somatic number of chromosomes in plants of the Europa clon are 24 (Strasburger, 1883; Timm, 1928), 32 (S. Nawaschin per Tischler, 1926), 33 (Belling, 1925), and 48 (Schürhoff, 1926). All of these estimates are based on studies of stages in sporogenesis in which, we find, there is frequent multiplication of chromosomes and of chromatin units, giving numbers much higher than the normal number of 12 present in somatic cells.

In discussing the reports of different chromosome numbers for *H. fulva*, Timm suggests that there are different races. It is, however, to be noted that all of the different numbers reported may be found in a single plant and even in a single anther. Our studies involve plants of the Europa clon obtained from Italy, France, Belgium, Holland, Sweden, England and various parts of the United States. All these plants are indistinguishable; all have normally 12 chromosomes in the cells of root tips; all have the same types, ranges and degrees of irregularities in sporogenesis. We find, hence, no evidence that there are different races in this particular group of plants.

It is now fully obvious that the irregular numbers of chromatin units that develop during sporogenesis in plants of the Europa clon make it necessary that a decision as to the number of diploid chromosomes in the tissues of the plant be based on studies of somatic divisions as well as of the early stages of meiotic division. But here also irregular chromosome numbers may occur as our figures show. Possibly this is true of numerous other plants now classed as polyploids.

INCREASE IN THE NUMBER OF CHROMATIN UNITS

A feature of special interest in the abnormalities of sporogenesis in plants of the Europa clon is the frequent increase in the number of chromatin units both by irregular segmentation and by splitting. Segmentation is seen in diakinesis and in the prophase and metaphase of the first meiosis. In extreme cases it may involve all the chromosomes.

The splitting of univalents during the first meiotic division, such as is seen in the Europa clon, has been observed in various plants. In fact, this behavior seems to be frequent in many hybrids and in many cases of polyploidy. It appears, however, to be the rule that the splitting which occurs in the first division is not followed by another splitting and that the total number of chromosomes is, hence, not raised above that which is normal for the total of the second division. Yet in these cases unequal distribution of the units may give greater or less numbers than the normal haploid number to certain of the spores and gametes.

Two splittings of single chromosomes during meiosis, such as are seen in Europa are apparently not frequent among plants. Such behavior has been reported especially for certain *Hieracium* hybrids by Rosenberg (1917) and for certain canina roses by Tackholm (1922). Karpechenko (1927 *a* and *b*) also reports a splitting of some of the univalents in the first division as well as in the second division, but he states that this very seldom occurs in his material. Karpechenko's studies are of special interest as reporting definitely the development of functional gametes with the somatic number of chromosomes or with higher numbers. In his F_1 hybrids between *Raphanus sativus* x *Brassica oleracea* the somatic number is 18 with 9 derived from each parent. Most frequently the number of chromosomes in gametes is 9 but these abort or are non-functional. Only a few spores are functional and these have 18 or more chromosomes—the numbers 18 and 36 being most frequent. The number 18 arises by the complete omission of a reduction division, followed by the organization of all the chromosomes into one nucleus, which divides in the second division of sporogenesis simply as a somatic division, giving two spores with 18 chromosomes each or in case of non-distribution with such numbers as 16 and 20.

Karpechenko also reports that pollen mother cells may contain two nuclei, whose chromosomes collect in one spindle, divide as in somatic divisions and give rise to two pollen grains with 36 chromosomes in each. This seems to suggest that the chromosome groups from the male and female parents of these hybrids have maintained group identity and not mingled as they usually do. One of Karpechenko's figures (his Fig. 17, 1927a) shows more than 70 chromosomes, a condition which he considered to be due to a "two-fold splitting of some univalents" or a splitting in the first as well as in the second division of meiosis. By such means the number of chromosomes is multiplied in certain cases to at least twice the somatic number. These extra splittings parallel those we have observed but we have seen no indication that two nuclei are present in the pollen mother cells of plants of the Europa clon.

Piech and Moldenhawer (1927), also working with hybrids between *Raphanus sativus* and *Brassica oleracea* but evidently with different strains, find an increase in the number of chromosomes during the first meiosis from 18 to as many as 36 by the splitting of univalents. They report no further splitting and they state that in the second division four spores are formed and that the number of chromosomes is thus reduced to 9. The second division is hence a reduction division. But irregular distribution or the formation of fewer than four spores may give more than

nine chromosomes to certain spores. Here evidently there is less irregularity than in Karpechenko's material.

In most studies of irregularities in sporogenesis attention has been directed chiefly to the irregular distribution that accompanies the presence of unpaired chromosomes. A double splitting with partial or incomplete separation such as is seen in the Europa clon may be more general than is now apparent.

TYPES OF STERILITY INVOLVING ABORTION OF SPORES

It is to be recognized that there are several types of germ-cell abortion in flowering plants, especially in respect to that condition or status of the plant which may, perhaps, be regarded as an underlying or fundamental cause of the sterility. On this basis the following classes of sterility due to spore abortion may be recognized:—

1. Abortion of sporophylls, of spores and of sex cells is a characteristic feature of *intersexualism*. In extreme cases of male sterility in intersexes the stamens are merely rudimentary organs, as in *Plantago lanceolata* (Stout, 1919). In certain other pollen-sterile plants, such as the Brighton grape (Dorsey, 1914), the abortion occurs after the formation of pollen grains by a degeneration of the generative cell or of the divisions that produce that cell. In such extreme cases of cyclic alternations in sex as are seen in *Cleome spinosa* (Stout, 1923) there is an alternating graded series of abortions in the development of the flowers throughout the flowering period. At one time the pistils are aborted and at another time the stamens are aborted, and in the climax the abortion of sporophylls reduces them to merely rudimentary structures.

The distinguishing feature in the intersexes is that the abortion is typically merely one-sided. There is an abortion of one sex while the other may be fully functional. In intersexes the abortion is obviously not due fundamentally to misfits in the relations of chromatin material or to the erratic behavior of chromosomes but to a loss of maleness or of femaleness through some fundamental systemic regulation that is regularly hereditary. Both as to expression and cause it is distinct from various other types of sterility which involve abortion of sex organs.

It is clear that the abortion of spores as developed in the Europa clon is not that of intersexes, for it obviously affects both microspores and macrospores to the same degree and at the same time.

2. Cytological studies of the pollen sterility of hybrids have been numerous since such earlier studies as those of Juel (1900) for *Syringa*

vulgaris, of Tischler (1906) for the hybrid *Ribes Gordonianum* (recently reinvestigated by Tischler, 1927) and of Rosenberg (1909) for *Drosera obovata*. Hybrids are frequently more or less sterile from abortion of spores and sex cells and this involves a rather wide range of nuclear and chromosome irregularities not only when the two sets of parental chromosomes are unequal in number but also when the numbers are equal.

There seems to be rather general agreement that in the sterility of hybridity the irregularities occur during meiosis, particularly in the non-pairing of univalents and in their subsequent irregular distribution. It is characteristic of the sterility of hybridity that the abortion develops to the same degree in the formation of both the microspores and the macrospores, which indicates that the abortion involves fundamentally incompatible relations between chromosomes.

In a recent paper Blaringhem (1928) considers that the Europa Day-lily arose as a hybrid. This view is based in part on the high degree to which abortion of spores occurs and in part on the results of his breeding experiments. In using pollen of Europa in crossing with *H. flava* he obtained plants of the first generation and also he grew a second generation, but all were yellow-flowered, as is *H. flava*. There was in their flowers no trace of the fulvous-red coloring characteristic of *H. fulva*. In further use of the pollen of Europa on flowers of *H. flava* and *H. auranteaca*, out of a considerable progeny only two had fulvous-red coloring in the flowers. Evidently these two plants were the only ones that were hybrids. These differed in vigor of growth and in sterility and because of this it was assumed by Blaringhem that the Europa parent is itself a hybrid.

In the breeding of day lilies at The New York Botanical Garden plants of *H. flava* have been highly self-compatible and also frequently self-pollinating before flowers open. But where flowers are emasculated in the bud before pollen is shed, the properly guarded pollinations with pollen of the Europa clon give in every case F_1 hybrids that possess considerable fulvous red in the coloring of the flowers. This is likewise the case for the reciprocal hybrids. In the next generation obtained by crossing F_1 plants or of back-crossing with Europa there has been great variation in vigor of growth and in the degree to which fulvous coloring is developed. This may mean that Europa is itself heterozygous or that the inheritance of its fulvous coloring is on the basis of multiple factors. The species to which the Europa clon belongs is a variable one, judged by the wild plants obtained from China and Japan.

Self-incompatibility is so strongly developed in the species that at least many plants of seedling origin are the result of cross-pollination between plants that differ in coloration. The Europa clon is evidently heterozygous for color of flowers, but there is no very conclusive evidence that it is a hybrid between two distinct species. Among the wild plants obtained from China and grown at The N. Y. Botanical Garden there have been some that very closely resemble the Europa clon, especially in respect to the color and shape of the flowers.

The abnormalities seen during sporogenesis in plants of the Europa clon closely resemble those common in hybrids, especially in the non-pairing, the nondisjunction, the irregular distribution of the chromosomes and the formation of extra numbers of pollen grains. The omission of the reduction division and the multiplication of chromosomes during the divisions are also quite similar to irregularities observed in certain known hybrids.

3. A rather extensive literature has recently appeared concerning the sterility of polyploids. It appears that the odd numbers of chromosomes in triploids, pentaploids and various aneuploids promote irregularities in meiosis which result in the abortion of spores. (See especially Blakeslee and Cartledge, 1927.) But here, as in certain hybrids, abortion may also develop in forms having sets of chromosomes of even number, which, however, seem to be "unbalanced" in the relations of meiosis.

Sterility in polyploids is undoubtedly a chromosome phenomenon coming to expression during meiosis. As a general rule, it develops in quite the same degree for both microspores and macrospores and hence is quite similar to sterility from hybridity. In certain cases, as in *Fragaria* (Longley, 1927), dioecious plants are found to be polyploid, but, as in such cases the chromosomal complex of a plant is fully potent in one sex, it would seem that such one-sided abortion is not merely due to the number of chromosomes involved.

Plants of the Europa clon are clearly not polyploid. In the somatic tissues the normal number of chromosomes is 12, which, it now appears, is the basic diploid number for the genus. In the chromosome irregularities there is an increase in the number of chromatin units, so that many of the cells become polyploid and aneuploid, and in this respect the abortion of spores may be similar to that which occurs in plants whose somatic cells are uniformly polyploid.

4. Abortion of spores is the rule for plants which produce seeds by parthenogenesis or by apogamy. The cytological studies of such plants

show very marked irregularities throughout the processes of sporogenesis. In reviewing these Sharp (1926, p. 356) has noted that there is "a series of transitional conditions between normal meiosis associated with sexuality and failure of meiosis associated with apomixis." It seems that a rather common rule of behavior in apogamic plants is that the egg mother cells merely continue in somatic divisions with slight signs, or even no signs at all, of the stages of synapsis and meiosis, while for the pollen mother cells there are such irregularities that the pollen is usually all aborted. Examples of this are the common dandelion (Jeffrey, 1927), and the hawkweeds, which have been studied by Rosenberg (1917, 1927).

In respect to many of the irregularities in sporogenesis, there is much similarity between the conditions found in hybrids, polyploids and parthenogenetic forms. In the latter, however, there is the ability to produce embryos vegetatively. Parthenogenetic and apogamic forms include both hybrids and polyploids, and the evidence of relationship is so strong that it has been considered by some (Ernst, 1918; Jeffrey, 1927) that hybridization and polyploidy of themselves frequently stimulate parthenogenetic tendencies in the ovule apparatus.

There is no evidence that plants of the Europa clon are in the least degree parthenogenetic or apogamic. The few seedlings that have thus far been obtained from them are the result of cross-pollination with other species and are obviously all hybrids.

5. In the four classes of plants mentioned above which exhibit irregularities in meiosis and abortion of spores, the fundamental condition responsible for the irregularities may be considered as inherent in the plants themselves or as inherent in some condition or set of interrelations between the mechanisms of the cells and particularly of the germ cells. A somewhat similar irregular behavior of chromosomes both in mitosis and in meiosis has in various cases been induced by subjecting plants to chemical influence (to chloral hydrate, Nemec, 1904), to mechanical treatment such as shaking, and to higher and lower temperatures than usual, all of which temporarily modify the physiological condition of the cells concerned in sporogenesis.

In considering the causes of pollen abortion in *Hemerocallis*, Timm (1928) emphasizes the possibility of the action of climatic influences. But it can scarcely be considered that a purely external influence, such as temperature, plays an important role in producing the high percentage of gametic sterility always and very constantly seen in plants of the Europa clon, as they grow rather widely in the North Temperate Zone.

At any rate, certain plants of the same species, plants of other species and certain seedlings of *Europa* parentage show little or no abortion of spores when grown under the same conditions.

6. The doctrines of plethoric sterility and of correlative sterility have frequently been evoked to explain cases of sterility of plants that propagate vegetatively. It has been claimed that there is a direct competition for food material between vegetative organs of reproduction and the organs concerned with seed reproduction, and also that the degeneration of sex organs may result from long-continued propagation by sexual means.

There is no conclusive evidence that any clon of plants such as *Europa* has changed from a condition of high sexual potency to a condition involving the degeneration of the sex cells because of extended vegetative propagation. The evidence indicates that the original seedling from which such a clon has been derived was itself as strongly pollen-sterile and egg-sterile as are the plants now grown of the clon. This, however, does not necessarily indicate that a correlative or a plethoric sterility may not be operating in the *Europa* clon, but only that, if it is operating, it was inherent in the nature of the original seedling.

Various individuals belonging to the same species as this *Europa* clon and also various seedlings having it as a parent are highly potent as seed and pollen parents. Also many individuals of various related species show little or no abortion of spores. The habit of vigorous vegetative reproduction, which is well developed in the genus, does not of itself necessarily induce abortion of spores and loss of sexuality.

THE INHERENT AND HEREDITARY NATURE OF SPORE ABORTION

For various types of sterility it is frequently the rule that there is an abortion of a rather definite proportion of the spores. In some cases the very constant proportions of spore abortion in plants and in their offspring have been interpreted in terms of hereditary factors conceived to be directly concerned with sterility (see especially Belling, 1914; Shull, 1927). With such a viewpoint the rather definite relation of about twenty aborted spores to one viable spore for sporogenesis in plants of the *Europa* clon may suggest the presence of multiple factors operating in the development of the haploid generation. At any rate, the rather definite degrees of abortion seen in various types of sterility indicate that there is some condition inherent in the plant that determines and regulates the percentage of abortion.

In hybridity the abortion is assumed to be determined by the interrelations of the chromosomes. In apogamy the abortion is obviously due to a very different condition or at least a further development, for there is loss of sexuality with the substitution of vegetative methods of seed formation, which maintains the nuclear organization of the somatic cells. In intersexes the chromosomal complex is of itself in no way directly responsible for the abortion that operates in only one of the two kinds of sex organs (pistils or stamens).

THE IMMEDIATE CAUSES OF SPORE ABORTION

A study of the fundamental nature of the cell processes involved in the destructive activities of spore abortion shows that they fall into a few simple categories whose essential characteristics and etiological relations can be viewed in the light of the known facts of cell growth and reproduction.

Spore abortion is largely predetermined by the events of fertilization. In fertilization there is the fusion of two nuclei, which may possess and very often do possess cytoplasm and germ plasm of very different hereditary and physiological properties. Also polyploidy, arising within a strain, may produce gametes that are quite different in quantitative as well as qualitative properties. That the interactions in fertilization may be destructive is well shown in embryo abortion. In some cases such abortion is so definite that the theory of balanced lethals may be applied. As Davis (1915, 1923) has pointed out, there may be a high degree of abortion of zygotes or embryos in hybrids and in such plants as certain of the *Oenotheras*, which are also somewhat characterized by irregularities in sporogenesis. Much embryo abortion is no doubt due to a decided lack of harmony in the interactions between protoplasmic units that become associated in the same nucleus through fusion. Fertilization is a critical point in ontogeny. It initiates an association of different elements of protoplasm that prevails and interacts throughout somatic divisions and culminates in the more complicated relations in sporogenesis.

Certain grades or degrees of differences in gametes will yield nuclear organizations in fertilization that apparently live more or less in harmony until sporogenesis is reached, when the abortion of spores becomes a conspicuous feature. The abortion is associated with the more intimate pairing of chromatin units in synapsis and with the return to the haploid generation. It is characterized by irregularities in chromosome behavior.

Sporogenesis is also a critical stage in ontogeny. It is equally critical, or perhaps more critical, than fertilization.

Irregularities in chromosome behavior are to be found, however, in the cell divisions of somatic tissues. In the root tips of the *Europa* clon abnormal chromosome numbers readily develop through non-distribution. Furthermore, we find no evidence that somatic nuclei which receive a low number of chromosomes or a number less than 12 can continue in division. For such cells there is cessation of division, which amounts to a tissue abortion. Such irregularities are without a doubt due to the expressions of the same sort of incompatibilities with which we are more familiar in the forms of sterility in reproductive organs. The behavior of chromosomes in the somatic cells of hybrids and of polyploids has been too little studied; it may be much more erratic than is now supposed.

The irregularities and abortions which appear in mitosis and in meiosis indicate that the destructive interactions develop especially when (a) chromosomes are in relations with kinoplasm, (b) when chromosomes are in processes of splitting or fragmenting and (c) when the activities of pairing and disjunction of chromatin units are in progress. The relations of kinoplasmic activities to chromosomes are important aspects of chromosome behavior in nuclear divisions. In somatic divisions the kinoplasmic activities complete nuclear division where non-distribution is very pronounced (Pl. I, Figs. 3, 4 and 5) and this may continue for certain cells that have received increased numbers of chromosomes. In sporogenesis kinoplasmic activities become very irregular. With the lagging of chromosomes in the first meiotic division micronuclei form, and many, or perhaps all of these, do not divide further. Cell plates form after the first division with the greatest of irregularity and, when there is much fragmentation and multiplication of chromosomes, there is delayed action of kinoplasmic structures.

The meiotic divisions are obviously more complicated than are somatic divisions both in the activities of chromatin and in the rôle of kinoplasm. Synapsis and the relations that follow between chromosomes bring chromatin elements into more intimate interactions than previously existed. Disjunctions and nondisjunctions bring new relations in nuclear organizations more varied or at least more intense than those of somatic divisions. It seems clear that it is the interactions between chromosomes or between parts of them that give rise to the degenerations in cell processes and to the abortion and death of cells. The abnormalities

suggest the poisonous or toxic actions of foreign proteins in colloidal relations.

In the somatic and the pollen mother cells of plants of the Europa clon there is normally a numerical equality in the two sets of chromosomes and there are no noticeable differences in the size and the shape of the chromosomes. The incompatible relations develop as inherent qualities of chromosomes that are balanced as to number. Yet there are fragmentations of chromosomes, failure of pairing, non-distribution, non-disjunction, division of univalents both in the first and in the second meiotic divisions, the formation of abnormal shapes in chromatin units, and the irregular formation of spores as to size, number and chromosome complement. Finally there is abortion, death or a non-functioning for nearly all of the sporogenous tissue. The fact that few functional microspores and macrospores are formed is, perhaps, an indication that only in a few cases do the chromosomes find themselves in mutually harmonious relationships as to number, form, complement, chemical and physical interactions, and perhaps relative position similar to those which existed in the gametes which united to make the individual plant from which the clon has been propagated asexually.

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PLATE I

The drawings for these figures were made mostly at magnifications of from 1800 to 2400. The reproduction here given is about two-thirds the size of the originals. All figures are of the *Hemerocallis fulva* clone Europa:—

FIG. 1.—Equatorial plate of somatic division showing the normal number of 12 chromosomes.

FIG. 2.—Anaphase of mitosis showing 12 daughter chromosomes passing to each pole.

FIG. 3.—Anaphase of mitosis with much non-distribution. Only 5 chromosomes are at one of the poles.

FIG. 4.—Anaphase of mitosis with at least a total of 40 chromosomes.

FIG. 5.—Anaphase of mitosis with a total of 56 chromosomes passing to poles in groups of 28 and 30.

FIG. 6.—A typical synapsis in pollen mother cells.

FIG. 7.—Diakinesis with 4 bivalents and 4 univalents.

FIG. 8.—Diakinesis with large and small chromatin masses, the total number being at least 17.

FIG. 9.—Diakinesis with at least 24 masses of chromatin of irregular sizes, some of small size.

FIG. 10.—Late diakinesis with 6 bivalents. The number of chromosomes is normal and all are in pairs.

FIG. 11.—Polar view of equatorial plate of the first division of reduction showing 6 bivalents, or 12 chromosomes, arranged in 6 pairs, a condition fully normal.

FIG. 12.—Equatorial plate of first division with 6 bivalents all of which are in the early stages of segmentation and fragmentation.

FIG. 13.—Equatorial plate of first division of meiosis showing 5 bivalents and 2 univalents, and FIG. 14, a sister nucleus in same stage and at same magnification, showing 12 univalents all in process of dividing.

FIG. 15.—Equatorial plate of first division with 6 bivalents showing considerable fragmentation.

FIG. 16.—Equatorial plate of first division with much fragmentation.

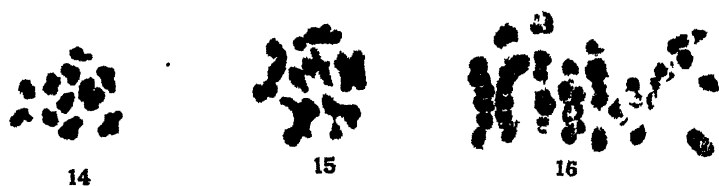


PLATE II

The drawings for these figures were made mostly at magnifications of from 1800 to 2400. The reproduction here given is about two-thirds the size of the originals. All figures are of the *Hemerocallis fulva* clone Europa:—

FIG. 17.—Metaphase of the first division showing 12 chromatin masses passing to each pole, with some split and some fragmenting.

FIG. 18.—Splitting and fragmenting of chromatin masses in the metaphase of the first division.

FIGS. 19 & 20.—Early anaphase of first division with a lagging chromosome.

FIG. 21.—Three groups of 4 chromosomes with some split, at the time of the anaphase of the first division.

FIG. 22.—Anaphase of the first division with cell plate forming and parts of one chromosome on opposite sides of it.

FIG. 23.—Anaphase of first division with the 6 chromosomes of each group split for the second division.

FIG. 24.—A condition after the equatorial plate stage of the first division. The chromosomes have fragmented and split and some are of irregular shape. The distribution is irregular. This condition follows that shown in Fig. 16.

FIG. 25.—A condition frequently seen following the anaphase of the first division with X-shaped chromatin masses developed.

FIG. 26.—One of two cells formed by the first division. The 6 chromosomes are split for the second division.

FIG. 27.—Two cells formed by the first division, one with 6 chromatin masses, the other with 12, some of which are split.

FIGS. 28 & 29.—Polar views of the two equatorial plates of a second division in reduction, one with 12 masses, the other with 16, and all in process of dividing.

FIG. 30.—An anaphase of the second division with four groups of chromatin masses of the numbers 12, 16, 17, and 18, with some of irregular shape and possibly double.

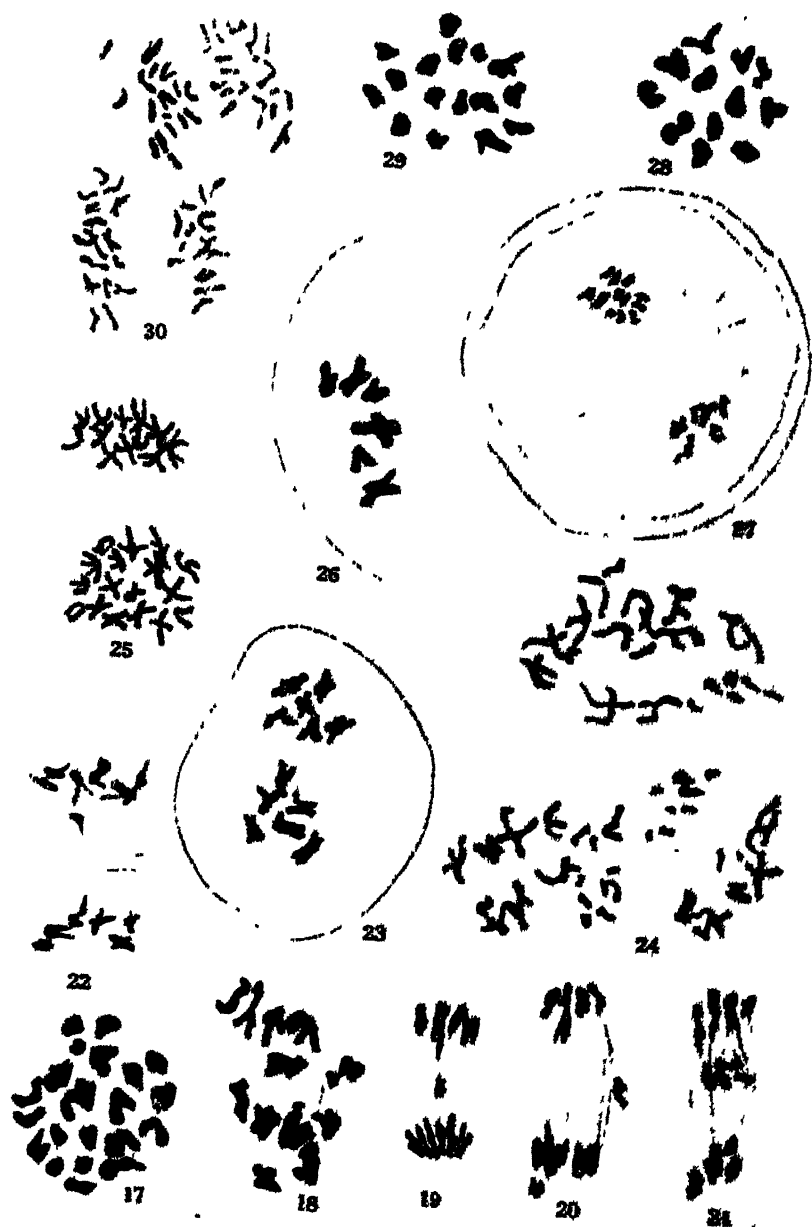


PLATE III

The drawings for these figures were made mostly at magnifications of from 1800 to 2400. The reproduction here given is about three-quarters the size of the originals. All figures are of the *Hemerocallis fulva* clon Europa :—

FIG. 31.—Anaphase of the second division. The chromosomes are nearly normal in shape and in total number, but they are being distributed into five groups of 3, 4, 6, 6, and 7.

FIG. 32.—Anaphase of the second division. The total number of chromosomes is normal, their shape is normal, the number of nuclei being formed is normal, but there is non-distribution in each of the two spindles.

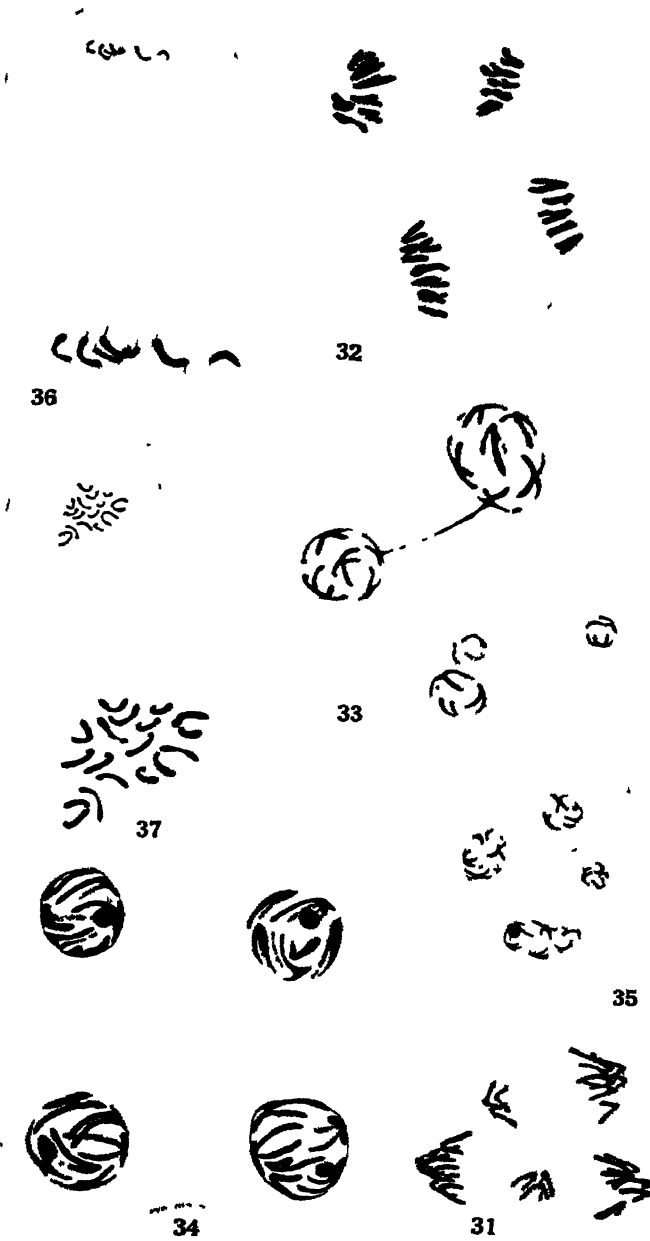
FIG. 33.—Five nuclei developed from one spore mother cell. They are of different sizes and contain X-shaped chromatin masses. Chromatin material is stretched between two of the nuclei.

FIG. 34.—A normal number of 4 nuclei following the second division.

FIG. 35.—Four cells of a quartet somewhat unequal in size and the nuclei containing X-shaped chromatin masses (magnified only 1000 X).

FIG. 36.—Microspore at the time of the division of its primary cell. There is the normal haploid number of 6 chromosomes. Below, the equatorial plate much more enlarged.

FIG. 37.—The same stage shown in Fig. 35 but the number of chromosomes is 18.



STUDIES IN CHELONIAN OSTEOLOGY

TRUSS AND ARCH ANALOGIES IN CHELONIAN PELVES *

Part I

By HERBERT RUCKES

CONTENTS

	Page
Introduction.....	32
Mechanical and engineering principles in the skeletal system.....	32
Historical résumé	33
Truss patterns of chelonian pelvis.....	35
Definitions and truss analysis.....	35
The chelonian pelvis as a truss.....	39
A standard aspect for the analysis of the pelvis.....	40
Three types of pelvis from the standard aspect.....	41
Analyses of the truss and arch in chelonian pelvis.....	44
Forces and stresses in the pelvis.....	46
Publischial forces and equilibrants in various types of pelvis.....	48
1) Triassochelys.....	48
2) Pleurosternidæ.....	49
3) Baenidæ.....	50
4) Chelydridæ.....	51
5) Emydidæ.....	52
6) Kinosternidæ.....	54
7) Chelonidæ.....	54
8) Trionychida.....	56
9) Pleurodira.....	57
Chelydidæ and Pelomedusidæ.....	57
The internal architecture of the pelvis.....	59
The arrangement and analysis of the trabeculae of the ilium.....	59
Laws of beams and columns.....	61
The arrangement and analysis of the trabeculae of the ilium.....	64
The ilium as a column: external aspect.....	67
The ilium as a column: internal aspect.....	68
The internal cancelli of the ilium.....	69
Cancelli of the distal portion.....	70
Cancelli of the middle third.....	71
Cancelli of the proximal portion.....	72
Comparisons with other types of illa.....	73
The graphic analysis of the cancelli of the ilium.....	74
Discussion.....	75
Conclusions.....	78
A. Truss analogies.....	78
B. Finer structure of the bone.....	79
Bibliography.....	79

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INTRODUCTION

MECHANICAL AND ENGINEERING PRINCIPLES IN THE SKELETAL SYSTEM

The structural plan of a vertebrate body follows a physical pattern based upon mechanical and engineering principles. While this fact has long been established, it is not so widely realized as it should be. Especially is this true of the skeletal system, in which bones are associated with one another and with the surrounding softer organs in much the same way as are the respective members of a system of levers, trusses or arches. The arrangement of skeletal elements falls under the influence of laws that are identical with those that govern the form and function of mechanical appliances and therefore are subject to the same methods of analysis; that is to say, the position and interrelationships of the skeletal parts are capable of being explained, at least in part, by simple mechanical and physical principles.

It has been shown that analogies between organic structures and mechanical appliances exist, but very little research has dealt, as yet, with the complete mechanical interpretation of any one system of skeletal elements and, so far as can be determined, no papers have appeared which deal with a graphical analysis of the structural differences occurring in the same parts of closely related animals. It is generally agreed that variations in habit and habitat are reflected in the shape, size, position and texture of skeletal elements. By studying these correlated data one should be able to explain what principles of mechanics and engineering are the underlying causes of whatever structural variations occur.

The writer has selected the Chelonia as an order of reptiles exhibiting unity as a natural group but including individuals that lead lives of very diverse character. They are consequently suitable subjects for investigations concerning variations in the mechanical relationships of the skeletal parts. It is the purpose of the present paper to attempt a more or less comprehensive analysis of such skeletal parts. As an analysis of the entire skeleton would involve too lengthy a discussion, attention has been centered on a certain limited region. For this purpose the pelvic girdle has been studied because it represents, in the estimation of the writer at least, one of the most variable portions of the chelonian skeleton. Within the different families of the order, the pelvis offers material for a study in extreme contrasts of construction and position of homologous parts.

HISTORICAL RÉSUMÉ

The present problem is more or less limited in its scope. It presents several general aspects that are important and probably applicable to the study of the mechanics of other skeletal regions. The general aspects must not overshadow the detail of the problem itself. Consequently, the historical résumé may be very brief if one considers the very small amount of work performed on the interpretation of the mechanics of the skeleton in the Chelonia, or it might be very extensive if one were to abstract all the literature dealing with the laws of skeletal construction and bone architecture. The fundamentals of physical and mechanical osteology have been carefully studied and described by investigators interested in the human skeleton. Most of the literature consequently deals with the topic of human bone construction.

Ward ('38) was one of the first observers to realize the value of the mechanical arrangement of bones in the body. His *Outlines of Human Osteology* is replete with diagrams and analyses of the leverage actions of the various parts of the skeleton. Moreover, he was the first observer to see that the internal composition of bone is an expression of its mechanical value. He recognized that bone (especially long bone) is composed of cancelli or trabeculae which (in the human femur) are arranged, according to his interpretation, in straight and parallel lines to support an overhanging load much as a cable suspended from a mast holds up the boom of a derrick.

Wyman ('57) basing his observations on the results of Ward's various papers, came to the conclusion that (in the human femur) the cancelli are not arranged in straight lines as Ward had supposed but are arcuate and arise from the ectal and mesal walls of the shaft. While this seems to be but a minor difference in opinion, from the mechanical point of view the differences in the pattern present views utterly opposed to each other. Wyman's interpretation has since been proved to be the correct one. Wyman further recognized the importance of the arching of the cancelli and explained that the arcuate fibers arising from the ectal wall of the shaft and passing through the neck and head of the femur represent lines of tensile stress within the body of the bone while those arising from the ental wall, passing more or less at right angles to the other cancelli, represent lines of compressive stress. Wyman then described a third set of cancelli, short ones, which he supposed were present in order that the tensile and compressive fibers might receive reinforcement and support. Since Wyman's time it has been shown

that no such third group of cancelli exists. Regardless of the correctness or incorrectness of Wyman's interpretation and observations, the fact remains that the later anatomists are indebted to him as one of the first workers in the field of physical osteology to point out certain underlying mechanical principles controlling the construction of bone.

Following Wyman, anatomists were stimulated to seek additional knowledge of bone mechanics and bone structure. In 1867 Culman, a Swiss engineer, became interested in the problems of bone architecture; while not a biologist, he contributed a great deal to the analysis, both mechanical and mathematical, of the femur. After making a careful survey of the structure of the femur, he constructed a mechanical model or analogue, known in the history of this subject as Culman's crane. This model purports to show in a purely mechanical object lines of compressive and tensile stress computed mathematically and accurately placed, which are almost exact counterparts of the lines represented by the trabeculae of the proximal end of the femur. Culman's principal conclusions were that not only do the cancelli represent lines of stress within the body of the bone, but that they lie along the paths of maximum stress and are so arranged as to transmit the maximum external load with the use of a minimum amount (volume) of organic material.

Since 1867 numerous papers of greater or lesser value have appeared; these confirm the work of Culman and his associates. The most outstanding work, that of Wolff ('92), pointed out the importance of the earlier work and reiterated the application of the mechanical and mathematical principles that underlie the internal and external architecture of bony elements. Wolff concluded from his own investigations that the internal organization of bone depends on and is determined by the static conditions present.

The most recent of all the papers dealing with this subject is that of Koch ('17). In his very extensive and intricate review that author gives a résumé of all the preliminary work in this field and then makes some remarkable additions to the knowledge already available. Koch is the first worker to contribute actual mathematical data (measurements and computations) to the analysis of bone. Culman had previously made a mathematical survey of stresses but applied his results primarily to his mechanical model. Koch used the human femur and procured all the necessary information (body weight, elasticity of bone, neutral axis of femur, etc.) to compute accurately the position of the stresses within the bone. From his investigation he concluded: a) that the form of the bone, both internal and external, results from a tendency toward adaptation to normal static demands, b) that the proportions of the skeletal

elements show definite mathematical ratios between body weight and the internal composition of the bone, c) that the particular bone in question possesses a certain factor of safety commensurate with its function or kinetic uses in walking, standing and running, and d) that the amount of bone present allows for the maximum resistant strength with the use of a minimum of organic substance.

Unfortunately there is a paucity of knowledge concerning the structure of bone other than human. Foote's ('16) paper on the structure of the vertebrate femur is one that deals primarily with the histological composition of bone. While the work is both extensive in its scope and intensive in its detail, it has practically no bearing on the present problem and is mentioned here only because it is one of the articles that deals with bone other than human. The fact that so little work has been done on non-human material is due probably to the greater interest aroused by the attempts to find out more and more about the human body, and by the diversion of effort to this end. The subject is no less important if applied to lower vertebrates and, in time, results of research may yield knowledge which, when used for the interpretation of human mechanics, will aid in a still better understanding of that complex problem.

In the present paper a modest attempt is made to show that analogous mechanical and mathematical principles underlie the construction of bone in lower vertebrates and that the relationships of bony elements to one another in these animals is much the same as in the human being.

TRUSS PATTERNS OF CHELONIAN PELVES

DEFINITIONS AND TRUSS ANALYSIS

As this paper is an attempt to apply the engineering viewpoint to a biological problem, it may be convenient to begin with a few definitions.

Mechanics . . . is that study in dynamics which treats of the laws of forces and the actions of forces on bodies.

Statics . . . that subdivision of mechanics which deals with the laws of forces acting upon solid bodies that are at rest.

Force . . . is an action upon a body that tends to change the state of rest or motion of that body.

Point of Application . . . that point on a body at which a force or the maximum force of a series is concentrated.

Line of action . . . a line or axis through a body or between two points of the body along which a force acts.

Stress . . . an internal force that resists external forces, and tends to preserve the original position of the units (molecules) that make up the body. Like forces, stresses are measured in weights, and result in producing a *strain* in the body.

Compression . . . a stress tending to prevent adjoining planes in a body from being pushed together.

Tension . . . a stress tending to prevent adjoining planes of a body from being pulled apart.

Shear . . . a stress tending to prevent adjoining planes of a body from sliding over one another. *Torsion* is a special type of shearing stress applied in a rotary direction.

Resultant . . . a force which will produce the same action as two or more co-planar forces and which acts in the same plane as the given forces.

Equilibrant . . . a force of the same magnitude as a resultant but acting in the opposite direction from the resultant.

Components . . . two or more forces which by their combined action produce a result equivalent to some given force.

Moment . . . a condition produced by a force tending to rotate a body around a point. It is equivalent to the product of the magnitude of the force by the perpendicular distance from the line of action of the force to the point of rotation. In order that a body may remain in equilibrium when several forces are acting upon it, the sum of all the forces about a point in that body must be equal to zero. ($\Sigma M (f.n) = 0$).

Truss . . . a simple built-up mechanical member in which a small number of component parts are arranged in such a manner as to support a load and give mutual support without distortion. Usually a truss is used to take the place of a girder or beam.

Arch . . . a mechanical appliance which might be considered as a multiple truss or as following the laws laid down for truss construction but applied to a large and indefinite number of members. Any arch can be resolved into a number of simple trusses, so that the mechanical composition of the arch may be interpreted.

Since the term truss is to recur several times in this paper, it is worth while to stop at this point and give a more detailed description of the device. A simple "king-post" truss serves well as an example (Fig. 1A). In this instance only three members make up the truss and these rest upon a base. This base may be considered either as a line or a plate called, in the terminology of the subject, the base line. Thus, upon the base line rest two oblique *struts* 2-1, 2-4 and a vertical *column* 2-3. The

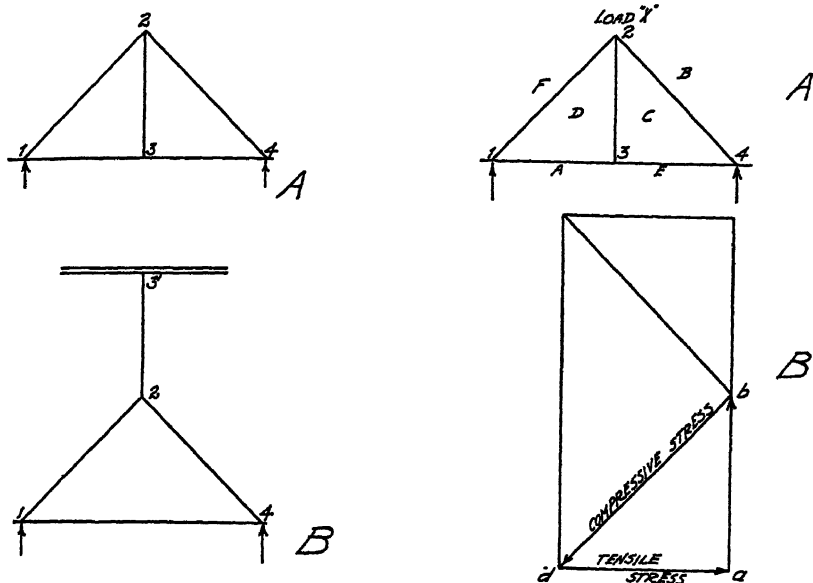


FIG 2.



FIG 1.

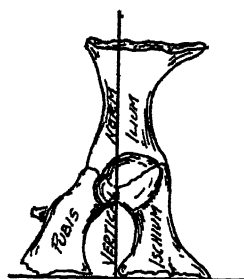


FIG 3.

FIG. 1A.—A simple "king-post" truss with 1-2 and 2-4 as lateral struts, 2-3 as the vertical column and 1-4 as the base line. The arrows at points 1 and 4 indicate reactions on the base line.

FIG. 1B.—A modified "king-post" truss in which the column extends to a superior supporting beam.

FIG. 1C.—The pelvis (sinistral view) of *Chelys* to illustrate the analogies of its parts with a truss.

FIG. 2A and 2B —The graphical analysis of the lines of action in a simple truss with the truss polygon (Fig. 2B) shown.

FIG. 3.—Side view of the pelvis of *Chelys* to show the position of the pelvis in the standard aspect. The vertical norm is drawn through the acetabulum perpendicular to the base line.

column is so constructed as to resist compression while the struts, obliquely placed, are continually under compression. Ordinarily such a truss is found in roofs and bridges, but the same resulting mechanical efficiency may be obtained if the column (2-3) projects in space above point 2. In such a case, however, in order to keep the truss in equilibrium, the end of the column (3') would have to be attached to an overhead support of some sort. Such a truss is considered as belonging to the second order and will be so called in this paper (Fig. 1B).

Let us return to Fig. 1A. At the apex of the larger triangle formed by the members of this truss is a concentrated load "X." The external forces acting upon this truss are: a) the concentrated load "X" acting upon point 2, and b) two reactions at the basal ends of the struts, indicated in the figure by arrows at points 1 and 4. The lines of action (stresses) within the members of the truss can be indicated by reverse arrows along the struts.

Forces acting within a truss do so in very definite lines of action. These lines can be determined for any truss by constructing what is called a force polygon. The polygon can be constructed only when certain data are known. The information must include the magnitude of the force, the direction of one force at least and the point of application of the known force. The force polygon is made beside the truss diagram, so that certain lines may be drawn parallel in the two figures (Fig. 2B). Thus, the force *ab* acts upon point 1. This force is drawn in its own line of action, its length representing its magnitude and an arrow indicating the direction of its course. The line *bd* is now drawn parallel to the member 1-2, starting at point *b*; the line *ad* is drawn parallel to the base of the truss starting at point *a*. The line *ad* intersects the line *db* somewhere in space. This point of intersection (*d*) is equivalent to point 1. In the truss all the forces have to be in equilibrium in order to maintain the stability of the structure; hence in the diagram all the forces of the polygon follow one another in counter-clockwise direction. ($\sum M (f.n) = 0$). Therefore the line of action along the left-hand strut is from point 2 to point 1. In like manner the lines of action in all the other members of the truss can be determined.

This analysis is of the greatest importance when one is dealing with a naturally formed truss as represented by the chelonian pelvis. As previously stated, the mechanical efficiency of the truss is not altered if the vertical column 2-3 is replaced by one in the position of 2-3', which extends in space from point 2 to be attached to some superiorly placed

support. The only difference this condition makes is that the line of action in the inverted column is reversed.

THE CHELONIAN PELVIS AS A TRUSS

From the point of view of mechanics the chelonian pelvis with its ilium, pubis and ischium represents a truss. The elements of the girdle are so arranged in the turtle as to become analogous to a truss of the second order. That is, the vertical column becomes the ilium and the two lateral struts are respectively the ischium and the pubis (Fig. 1C). The ilium extends superiorly from the acetabulum and becomes attached to an overhead support (the vertebral column and the carapace), as is required in a truss of this type. In the simple king-post truss it is assumed that a concentrated load is carried by the apex of the truss frame; in a truss of the second order the concentrated load is carried at the point of intersection of the three members of the truss. In the chelonian pelvis can be found an analogous condition, in which the concentrated load is applied at the acetabulum, having been carried to this place by means of a thrust of the femur. The forces will be distributed, then, from this point of application through the various parts of the truss. The above analogy is readily demonstrable if the pelvis is studied from the lateral aspect (Fig. 1C). If the pelvis is examined from the cranial side, an entirely different pattern and truss analogy is recognizable. Attention is drawn first to the lateral aspect.

The ilium is most like a member of a simple truss, being a somewhat elongated cylindrical body. The pubis and the ischium, while totally analogous to the lateral struts, are usually not cylindrical structures such as would be found in a simple truss, but are modified into more or less broadened plates. The necessity for this modification will be pointed out when the pelves of the respective families of the Chelonia are discussed. Regardless of the morphological nature of the individual parts of the pelvis, the important point is that lines of action of forces pass through the respective members just as they would pass through analogous parts of a truss. When a concentrated load is carried to the acetabulum by way of the femur, that load is in the form of a force. When the force enters the pelvis, it is broken up into its components, which are distributed to the various parts of the pelvis; each of these parts in turn resists the strain by virtue of the compressive and tensile stresses developed in its body, and the entire weight of the animal is distributed in three directions determined by the position of the members of the girdle.

Under other conditions the pelvis may be considered as a brace between the carapace and the plastron. In such a case the concentrated load is applied at the sacral region of the ilium and the line of action of the force (weight of the carapace) is carried ventrally through the ilium to the acetabulum, where it is broken up into its two components, each to take its course through either the pubis or the ischium. On the other hand, should the plastron tend to pull away from the carapace, the pelvic truss is present to offer the tensile stresses sufficient to prevent such a movement.

In the case first described, where the concentrated load is applied at the acetabulum, a tri-radiate truss, such as the pelvis is, would tend to collapse were not some provision made to keep it stable. By virtue of extensions developed on the mesal (inner) surface of the pubis and ischium, the girdles on the two sides of the body are permitted to abutt upon one another giving mutual support and forming a secondary multiple truss or arch (inverted), which prevents the shifting of either half of the pelvis out of its normal position.

In the mechanical construction of a truss the members are arranged in a very symmetrical pattern so that external forces and stresses (as compressions, tensions, shears and reactions on the base line) will be equally distributed throughout the structure. In a mechanical truss under the conditions prescribed the application of external loads is rather constant. In a natural truss such as the pelvis, the application of the concentrated load varies due to the constant shifting of the body during the act of locomotion. Unless the upper and lower extremities of such a natural truss are definitely fixed and immobile, it cannot be expected that the truss pattern will be always symmetrical. In fact, in only a few of the more highly specialized Chelonia (Pleurodira, Fig. 1C) does the pelvis possess a plan that approaches symmetrical proportions. By virtue of the inequality of the length of the pubis and ischium, the panels between these members become unequal in order to compensate for the variability and the range of the different external lateral stresses applied to the girdle.

A STANDARD ASPECT FOR THE ANALYSIS OF THE PELVIS

In order to maintain a standard of analysis for the girdles of the various families studied, it is necessary to view the pelvis from some standard or constant aspect. For this purpose, the following rule is adopted. It will be assumed that the pelvis rests upon a base line

(representing the plastron) which is tangential to the two most ventral points respectively of the pubis and ischium. Both of these members have processes that extend somewhat ventrally to the remainder of their bodies: in the pubis the lateral, ventral outgrowth is termed the pectineal process, while in the ischium the analogous process is called the ventral median or posterior ischial process. When the pelvis is in the position described, the standard aspect is more definitely established by making a point on the acetabulum (determined by the center of the line of intersection of the three planes respectively of the ilium, pubis and ischium) lie in a vertical normal drawn to the base line (Fig. 3).

THREE TYPES OF PELVES FROM THE STANDARD ASPECT

Under the fundamental assumption of a standard aspect for the analysis of the girdle, chelonian pelves fall into three categories. The first of these is that type of pelvis in which the ilium lies anterior to and almost entirely outside of the vertical normal drawn to the base line. The pelvis of *Triassochelys* (Fig. 4A) is apparently of this type. The second group consists of those forms in which the vertical norm lies within the body of the ilium although not necessarily coinciding with the morphological or centrally placed axis of that member. Various unrelated genera fall into this category, including certain Baenidæ, certain Emydidæ and all the Pleurodira (Figs. 3 and 4B). From the second category there are gradual transitions into the third, in which the forms are so constructed that the vertical norm passes through only the basal portion of the ilium and from there extends upward (dorsally), entirely outside of the morphological axis of the ilium and always craniad of that member. The great majority of the recent species fall into this group (Fig. 4C). The relative position of the ilium and the vertical norm seems to be an expression and indication of the direction of the thrust upon the whole pelvis. Two factors apparently enter into the determination of the position of the ilium. First, the mode of locomotion (terrestrial, palustral, aquatic) prescribes the establishment of a definite arrangement of bony parts and the composition of the internal nature of the bone. Secondly, the chelonian body is encased in a carapacial and plastral shell, the added weight of which is carried by the pelvic girdle. The range of variation of the directions and magnitude of the different thrusts from the limbs in locomotion and the shell in a resting stage must be reflected in the arrangement of the parts of the girdle.

In *Triassochelys* the concentrated load of the body acts from two centers; the carapacial shell thrusts upon the ilium at its sacral attach-

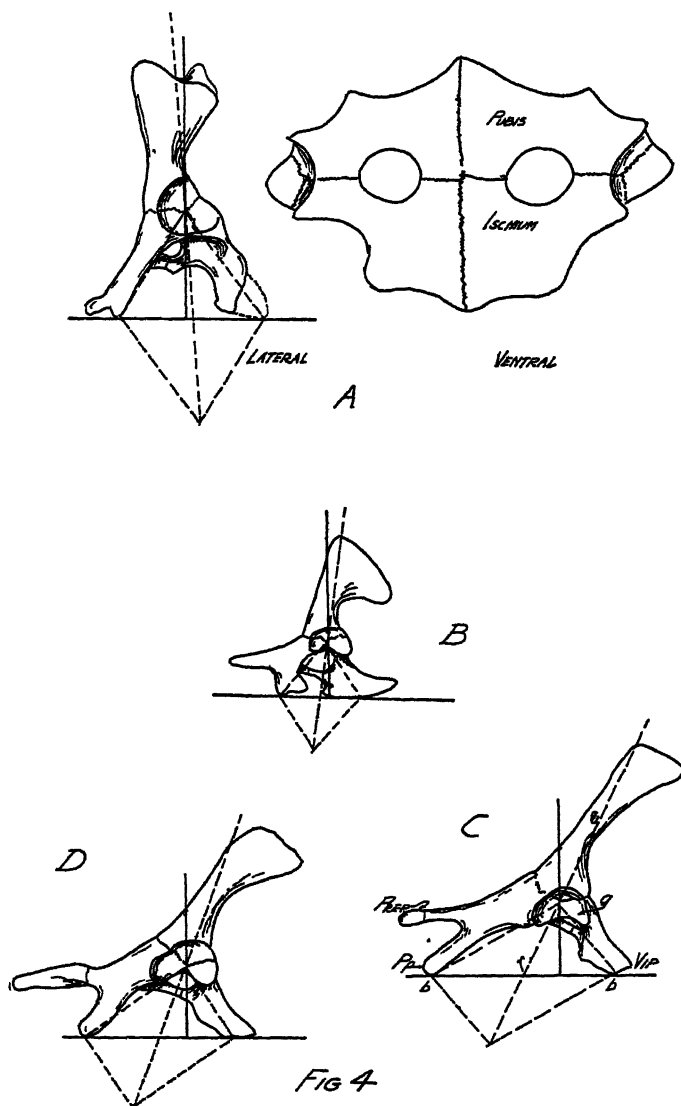


FIG. 4A.—The lateral and ventral views of the pelvis of *Triassochelys* (modified from Jaekel) illustrating group 1 of the types of pelvis studied. The vertical norm passes well through the posterior part of the ilium. The ventral view illustrates the difference in the size of the pubis and ischium.

FIG. 4B.—Pelvis of *Baena arenosa*.

FIG. 4C.—Pelvis of *Chelydra serpentina*. Abbreviations: a. acetabulum, b. most ventral points on the pubis and ischium, e. equilibrant, Pp. pectineal process, Prep. pre-pubic process, r. resultant, Vip. ventral inferior process of ischium.

FIG. 4D.—Pelvis of *Macrochelys temminckii*.

ment, while the body weight is thrust obliquely from the posterior direction into the acetabulum by means of the femur. The carapacial thrust is apparently from the anterior to the posterior and respectively from dorsal to ventral. In the pelves of the second category this carapacial thrust is practically vertical, while in those of the third group it is from posterior to anterior and respectively from dorsal to ventral.

Since the dorso-ventral thrust upon the ilium does not cease when the force reaches the acetabular end of that bone but is continued throughout the ischium and pubis, a correlation can be expected to appear between the positions of the two latter members and the ilium. *Triassochelys* exhibits the peculiar condition where the ischium is considerably larger than the pubis; this, undoubtedly, is due to the fact that the oblique thrust through the ilium causes the stresses to be unequally distributed in the two lower members of the girdle and, since the thrust in the ilium is in a specific direction (i. e., from anterior to posterior), the ischium takes up the greater amount of the stress distributed to the lower half of the girdle. Relying upon the fact that the bony architecture of the ischium and of the pubis is essentially the same, it is to be expected that the unequal stresses in these two elements will cause the one taking up the greater load to be of greater size. *Triassochelys* is the only turtle in which the size relation of the ischium to the pubis is of the proportion described and in which the ilium lies entirely (or nearly so) anterior to the vertical normal drawn through the acetabulum and the base line.

In the pelves of the second order (Figs. 3 and 4B), the rather vertically placed ilium distributes its stresses more or less equally to the pubis and ischium. It might be expected, then, that the lower two parts of the girdle would be of about equal size. This condition, in fact, is well borne out in the case of the Pleurodira and is closely approached in other representatives that possess pelves in which the central axis of the ilium and the vertical norm coincide. Usually in this group the pubis is larger than the ischium but not excessively so; the two elements are much more alike in size than in either the preceding or succeeding types of girdles.

In the third group of pelves (Fig. 4C) the pubis is by far the larger of the two ventral elements and proportionately increases in size as the ilium thrusts more and more from an oblique posterior direction. Underlying the construction of this pelvis are the same principles which determined that of *Triassochelys*, except, of course, that some of the lines of action enter this pelvis from different angles than in the case of *Triassochelys*. In *Testudo* the ilium is not carried obliquely posterior to

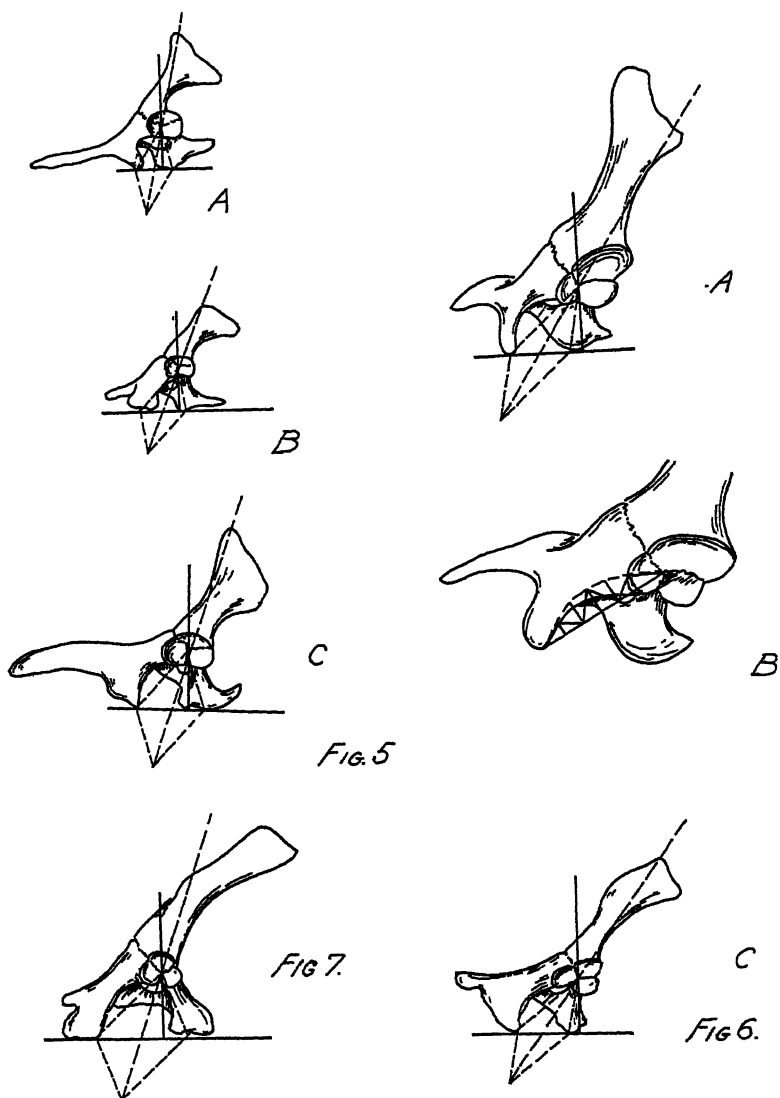
any great extent, and the pubis and ischium are subequal. In the land tortoises, however, the pubis is much smaller (proportionately) than in such forms as *Trionyx*, *Chelone*, *Dermochelys* and other swimming turtles, in which the ilium is carried far to the posterior and is very obliquely placed underneath the carapace.

The three orders of pelvis that have been described are by no means so sharply defined and distinct as might be imagined from the foregoing outline. There is a perceptible intergradation between the orders, as can be demonstrated in several instances. In a series from the Baenids to the Chelydrids, *Baena arenosa* (A. M. N. H. 5973, Fig. 4B) falls completely in the second order; *B. sima* (A. M. N. H. 5907, Fig. 5A) has a vertical norm lying more or less tangentially along the cranial edge of the ilium; *Glyptops plicatulus* (A. M. N. H. 336, Fig. 5B), a member of the Pleurosternidæ, has a vertical norm that cuts through the ilium about midway along the latter's axis; *Chelydra* and *Macrochelys* (Figs. 4C, 4D) have norms that cut across the ilium respectively about one third and one fourth of the distance from the acetabular end of that member, while *Chisternon hebraicum* (A. M. N. H. 5904, Fig. 5C), a member of the Baenidæ, has the ilium extending well posterior to the norm so that the latter line cuts through the ilium about one sixth of the distance from the acetabular end. Coincidentally with the backward shifting of the ilium the pubis becomes progressively larger and develops pronounced pre-pubic protuberances; the ischium, on the other hand, becomes relatively smaller and smaller.

ANALYSES OF THE TRUSS AND ARCH IN CHELONIAN PELVES

When the girdle is studied from the standard aspect, two problems present themselves. Each half of the pelvis may be considered separately or the combined halves (the complete girdle) may be surveyed as a unit. It is probably simpler to describe first the right or left half of the pelvis, and then with the knowledge thus gained interpret the composition of the entire girdle.

To reiterate, when seen from the lateral aspect, the pubis and ischium of the chelonian pelvis form the lateral struts of a truss while the ilium becomes the more or less vertically located column that must be placed in such a position as to connect with an overhead girder (the carapace and vertebral column). It is important to remember that the pelvis designed along these lines produces a truss pattern of the second order. When observing pelvis of the representatives of different families, one is

FIG. 5A.—Pelvis of *Baena sima*.FIG. 5B.—Pelvis of *Glyptops plicatulus*.FIG. 5C.—Pelvis of *Chisternon hebraicum*.FIG. 6A.—Pelvis of *Testudo pardalis*.FIG. 6B.—Detail of the pectineal process of the pubis in *Testudo* to illustrate the analysis of the arch and the determination of the chord of the arch to represent the line of force acting through the pubis.FIG. 6C.—Pelvis of *Cistudo carolina*.FIG. 7.—Pelvis of *Kinosternon*.

immediately impressed with the great diversity exhibited in the spatial relations of the pubis and ischium. In many terrestrial forms these two elements form a high narrow archway directly under the acetabulum (*Testudo*), while in the purely aquatic forms (*Chelone*) this archway becomes flattened out and very wide. In each case the arrangement of the particular elements is apparently a direct expression of the variations of the external stresses carried to the pelvis by the femur, which moves in definite respective planes and about definite axes of rotation. There also appears to be a close correlation between the proportions of the ischic-pubic arch and the depth of the body in the pelvic region. The high-domed land tortoises possess a center of gravity placed high in the body; this condition calls for a narrow but high-arched pelvic support, which must compensate for the great compressing and shearing stresses applied here. The flat-bodied marine and river turtles, with a shell modeled upon streamline patterns, have the center of gravity of the body fairly low. Such a condition does not produce the tremendous stresses found in the land types, so the pelvis compensates for the reduced vertical stress and becomes so arranged as to accept longitudinal stresses applied from the anterior and posterior directions.

FORCES AND STRESSES IN THE PELVIS

As long as the truss is symmetrically constructed, its graphical analysis is rather simple. By means of a force polygon the lines of action and the forces at work within the truss can be readily determined (c. f., page 37). When the truss has lost its symmetrical proportions, the analysis is less simple and can be approached more easily from the point of view of elementary mechanics than from principles of engineering. In such an instance we would be dealing not with a stress polygon but with the components, resultants and equilibrants of forces acting through the different axes of the elements that make up the truss.

The half pelvis of the turtle is a symmetrical truss in only a few instances (*Pelusios*, *Podocnemis* and *Chelys* (Figs. 1C, 3); even then the pattern is not perfectly symmetrical. In most *Chelonia* the pubis is consistently larger than the ischium; the ilium is not placed vertically in the body but rests rather at an oblique angle to the rest of the pelvis. The interpretation of a truss of this pattern becomes somewhat simplified by the application of graphic methods of analysis.

When two or more forces are applied to a point, their combined action can be expressed in terms of one single force, the resultant (r), which produces the same effect upon the body as was produced by the original

forces. If the point or body to which the forces are applied is to be kept in equilibrium so that the equation, $\sum M (f.n) = 0$ is true, then there is an equilibrant (*e*), equal in magnitude to the resultant but acting in the opposite direction. In a chelonian pelvic truss, the lines of force acting through its lateral members can be resolved into a parallelogram of forces the diagonal of which represents the force resisted by the third or middle members of the truss. In a mechanically constructed truss this line of action not only passes through the middle member of the truss but in that member passes through a series of points that represent the centers of gravity of any and all of its cross-sections. In this way the third member gives a maximum resistant value around the line through which the force is carried. (Cf. Section on stresses and neutral axis.)

The mechanical analogy of the chelonian pelvis is more fully appreciated when the analyses of the forces in its various parts are made and the results graphically shown. In *Macrochelys* (Fig. 4C), one of the Chelydridæ, for example, the pectineal process of the pubis and the ventral median process of the ischium rest upon the plastral plate, although they are not fused with it. The places where these two members of the girdle touch the plastron are the points of application of external forces or reactions on the truss, and the lines of internal resistant force will therefore travel along the courses of the two members in an oblique dorso-ventral direction. Starting at the point of union of the pubis and ischium within the acetabulum, the forces can be represented by the lines *a* and *b* drawn through the lengths of each member. From these two lines the parallelogram is constructed so as to give the direction (not the magnitude) of the resultant of the two forces applied. It is impossible to determine accurately the magnitude of any force in the pelvis since the absolute value of the forces is not known; an assumed value might be given but for the purpose of this paper would be entirely irrelevant. The direction of the force applied is easily determined by computing the centers of gravity of the various cross-sections of the different members of the pelvis. From what has been stated regarding the passage of forces within the members of a truss, it will be seen that the line joining the centers of gravity of the various sections coincides with the line of force passing through the respective member, thus representing a theoretical line about which are built up lines of stress. (Cf. Section on stresses.)

If, now, from the drawn figures of the parallelogram, the resultant (*r*) and its equilibrant (*e*) are constructed, it is a simple matter to determine through which part of the girdle the equilibrant passes, what

relation the equilibrant has to the centers of gravity of the various sections of that member, thus indicating whether or not the ilium, as the third member of the truss, takes up the effects of the forces carried by the pubis and ischium.

In each of the various pelves examined, representing the more prominent genera and families of Chelonia, it is found that the equilibrant of the pubic and ischial forces takes its course through the greater part of the ilium. In some instances (*Chelys*, *Pelusios*, and probably *Glyptops* and *Baena arenosa*) the equilibrant passes through the ilium in a line almost coincident with the axis connecting the centers of gravity of the different regions of the ilium. In other cases (*Testudo*, *Pseudemys*, *Chelydra*, *Kinosternon*, et al.), the equilibrant still extends through the greater part of the ilium close to the axis of gravity but does not coincide with it; however, the close parallel between these two lines is such as to cause no serious defects or weakening in the girdle or any part of it. So far as observed, in the most extreme cases these two lines are never more than 20° apart and consistently, when such cases exist, the equilibrant always cuts across the axis of gravity somewhere near the middle of the latter's course, so that the second resultant constructed from these two lines of force at work in the ilium once more would come to lie within the body of that member.

The conclusion that must be reached from the foregoing generalization is: that the ilium varies its position and inclination in the body partly to compensate for the variations in size and position of the pubis and ischium. These in turn, with their various proportions, may be controlled by the increase or reduction in size of some of the pelvic muscles *e. g.* pubo-ischio-femoralis-externus. But we cannot overlook the correlation between the position of the lower elements of the girdle and the inclination of the ilium, and it certainly seems that as the pubis and ischium approach the vertical norm drawn through the acetabulum (incidentally producing a high and narrow lateral archway between themselves), the more vertically must the ilium be placed so that the equilibrant of the pubic and ischial stresses can lie as closely as possible to the axis of neutral stress of the ilium.

PUBI-ISCIAL FORCES AND EQUILIBRANTS IN VARIOUS TYPES OF PELVES

1) TRIASSOCHELYS

(Fig. 4A)

In this form the main body of the ilium lies craniad of the vertical norm drawn through the base line and the center of the acetabulum. The

resultant of the pubi-ischial forces is applied at the acetabulum from the ventral and posterior aspect. Hence the equilibrant lies within the ilium but passes craniad of the vertical norm.

At this point it is necessary to digress from the descriptions of various pelves in order to explain an engineering principle that satisfactorily answers the question concerning the range in deviation of the equilibrant from the central axis of the ilium. Since the ilium is considered as being an analogue of a column, it is built of three hypothetical members, which lie side by side and extend the length of the structure. One of these members is considered to be a central or core member, the other two lying to each side of it. If stresses are carried by all three members of such a column, the resistant strength is said to be at its maximum. However, sufficient resistant value to withstand external forces can be obtained by having the lines of force pass through only the middle of three such hypothetical members, but the lines of force must pass through some part of that member if they do not pass through all three. In order to have a column in the form of the ilium that will withstand the range of stresses that are to be applied normally to the column, the lines of force as represented by the equilibrant of the pubi-ischial stresses must pass through some part of the middle member of an hypothetical three. The equilibrant does not necessarily have to coincide with the central axis of that member but to produce the desired resistant value it has to pass through at least some part of the member.

In *Triassochelys*, the equilibrant lies within the third or middle hypothetical member, though the axis of the latter and the equilibrant do not coincide. In this pelvis it was necessary to reconstruct a bit of the posterior and ventral part of the ischium, as this had been lost in the fossil; fortunately the remainder of the pelvis is so well preserved that it offers excellent material for analysis.

In *Proganochelys* and other Archichelydia the pelvis is not known well enough, so that no discussion of these forms can be given here.

2) PLEUROSTERNIDÆ

(Fig. 5B)

The oldest pelvis in the collection of the American Museum of Natural History is that of *Glyptops plicatulus* (A. M. N. H. 336) from the Morrison Beds of the Jurassic. While in some respects it represents the plate type of pelvis, it is certainly arched much like the pelves of the Beanids and Chelydrids. The archway between the pectineal process of the pubis and the lateral cranial edge of the ischium appears high but narrowed

anteriorly-posteriorly, a character which suggests a more terrestrial than aquatic habitat for these forms. The *Glyptops* pelvis belongs to the third of the three categories mentioned in the earlier part of this paper: that is to say, the vertical norm drawn through the base line and the center of the acetabulum lies cranial of the main part of the ilium. Due to the narrowness of the lateral arch, the pubi-ischial forces act through a comparatively small panel; but the resultant acts upon the acetabulum from the ventral anterior direction so that the equilibrant passes dorsally and posteriorly through the middle hypothetical member of the somewhat caudally extending ilium.

3) BAENIDÆ

(Figs. 4B, 5A, 5C)

The pelves of the representatives of this family form a very interesting series in that they lead rather gradually into the type of the Chelydrid pelvis. The principal similarity between the girdles of the Baenids and Chelydrids is in the presence of a prolonged pre-pubic process, which gives a decidedly wedge-shaped form to the entire anterior half of the structure. The main point of dissimilarity, however, is apparent when the girdles are viewed from the lateral aspect. The Baenid pelvis possesses a high and narrow arch, which probably reflects a terrestrial life, while the Chelydrid pelvis is provided with a low squat arch, which seems to be constantly associated with a more aquatic life. In the Baenidæ the pectineal process of the pubis remains close to the vertical norm, while in the Chelydridæ it has migrated anteriorly, taking the proximal portion of the pubis with it and giving greater flatness to the whole girdle. So long as the proximal portion of the pubis remains in a high arched position, the articulation between the median part of the pubis and the ischium remains broad and strong. This is the very condition found in the Baenidæ. Such an articulation between the two ventral elements of the girdle helps to establish a greater resistant value for the pelvis when it reacts to the horizontal stresses that are applied to it.

Within the family Baenidæ, there is a gradual shifting of the ilium to a more posterior and oblique position. The change in position may be seen in passing from *Baena arenosa* to *B. sima* and then to *Chisternon hebraicum*. It is entirely possible that the change in the inclination of the ilium is indicative of the variation in the modes of life of the different species; the more upright ilium of *B. arenosa* reflecting adaptation to a rather terrestrial life whereas the more inclined ilium of *Chisternon* indicates a form probably more palustral.

4) CHELYDRIDÆ

(Fig. 4C)

Several remarks have already been made concerning the two prominent species, *Chelydra serpentina* and *Macrochelys temminckii*, which represent this family. In addition it might be mentioned that the rather typical aquatic habit of these forms is evidenced in the much inclined ilium and the pronounced anteriorly displaced lateral arm of the pubis, which displacement produces the squat wide pubi-ischial arch found in other aquatic Cryptodira. The movement of the hind limb, producing an anterior-posterior movement, describes a more or less horizontal arc, which causes a longitudinal pull on the pelvic muscles, especially on the pubo-ischio-femoralis-externus. In order to compensate for this pull the pubis has to become prolonged to fit hypertrophied muscles; in doing so it moves away from the ischium and, growing in an anterior direction, breaks the symphysis where the two (pubis and ischium) articulated in the mid-central part of the pelvis.

A question might be raised as to whether or not the Chelydrid pelvis illustrates the low and primitive position of this family in the evolutionary scale of the Chelonina. The intergradation of the pelvic pattern of the Baenidæ and Chelydridæ seems to suggest such a position. On the other hand, there is a perceptible gradation of the Chelydrid pelvis to the pattern found in the Cheloniidæ. By the examination of the pelvic plan alone, it seems that the Chelydridæ stand about half way in the scale of adaptive radiation between the more terrestrial Baenidæ and the wholly marine Cheloniidæ. The present writer considers the Chelydrid pelvis as an aquatic modification of the Baenid type, while the Cheloniid pelvis represents the same evolutionary or adaptive trend carried to a greater degree and probably starting from another source.

In the Baenidæ the median portion of the pubis extends far beyond the pectineal process found on the side of that element. By the time the pattern changes in the Baenidæ from *B. arenosa* to *Chisternon hebraicum* the pectineal process encroaches upon the area occupied by the pre-pubic region; as a result there is no longer that disproportionate appearance of the anterior half of the pubis. The changes in the Chelydrid pelvis start at about the place where the Baenid changes leave off, hence there is not a very great difference in the truss pattern between *Chisternon* and *Chelydra*. *Chelydra* has carried the change to the degree where the pubis is pulled sufficiently far forward to rupture the ichio-pubic symphysis and replace it by a heavy ligamentous band, which in some of the Chelydridæ

(*Macrochelys*) becomes ossified. The ossification, undoubtedly brought about by the necessity of having the tensile and compressive stresses between the pubis and ischium taken up by some solid material, provides a strut between the two elements. The compressive and tensile stresses in the Chelydrid pelvis would occur all the time, but would reach their maximum proportions when the animals migrate overland to reproduce or to pass from one water course to another.

5) EMYDIDÆ

(Figs. 6A, 6B, 6C)

The pelvic pattern in this large family varies greatly because the respective species lead their lives in a diversity of habitats. Pelves are found varying from the low squat arched type with fairly well inclined ilia to those with high narrow lateral arches and nearly upright ilia. *Emys*, *Chrysemys*, *Deirochelys*, *Pseudemys* and other terrapins that are more aquatic than terrestrial illustrate the former of these two extremes while *Cistudo*, *Kinixys* and *Testudo*, of purely terrestrial habitat, represent the latter. The fact that all of the more aquatic species in this family migrate over land great distances during the breeding season is indicated by the retention of a girdle that is not of the extreme swimming type, but more or less approaches the pattern so characteristic of the terrestrial forms. In none of the more primitive genera (*Pseudemys* et al.), however, is the ischio-pubic portion of the pelvis markedly arched or bowed, but retains more of a platelike form. When *Pseudemys* is compared with *Testudo*, the platelike nature of the ischio-pubic region of the former is seen to be strikingly unlike the bowed or buckled ischio-pubic region of the latter.

Intermediate forms between the two extremes are to be found in the pelves of sylvan and campestral species. Moreover, there appears to be a gradual change from one extreme to the other. *Chelopus insculptus* lies at one end of the series and is more closely patterned after the type of the *Pseudemys* pelvis, while *Cistudo* lies at the other end and considerably resembles the *Testudo* type.

No matter what type of pelvis is taken as representative of the family, the general rule of truss analogies previously described holds true. In each instance the equilibrant of pubi-ischial forces acting through the lower half of the pelvis lies within the body of the ilium and very closely approximates the middle of the three hypothetical members of that element.

In the high narrow arched type represented by such forms as *Testudo*, it is necessary to construct an hypothetical arch along the lateral edge of the pubis so that the lines of force acting within the arch can be resolved into a chord subtending the arch and extending from the central region of the acetabulum to the ventral limit of the pectineal process. Within the panel so constructed, a series of hypothetical trusses can be created. When these are completed, they illustrate the fact that the chord subtending the arch is equivalent to the mutual base line of the total number of trusses constructed. The base line then represents the line of action of forces at work in the trusses and so is graphic representation of the course of the force passing through the lateral arch of the pubis. An analogous chord is constructed upon the less arched ischium. The two straight lines are then used as the sides of a parallelogram from which the equilibrant is determined.

In the land species of the Emydidae the most characteristic feature of the pelvis is found in the bowing or buckling of the ischio-pubic portion. The arching occurs in the anterior-posterior direction as well as in the right-left direction, and is due to the tremendous thrust exerted by the femur in the region of the acetabulum. In aquatic animals the body of the organism is buoyed up by virtue of the water pressure and the weight of the animal is not carried solely by the pelvic girdle and its limbs. In terrestrial forms, on the other hand, there is no counter action produced by the environmental medium, hence the entire weight of the body is carried by the pelvis and the limb. The greater relative weight the animal possesses, the greater will be the stress upon the pelvis; therefore in the heavily constructed land tortoises it may be expected that the girdle will react in its development so as to produce the most efficient type of supporting structure. Aside from the body weight of the animal and its method of support, another factor controlling the construction of the girdle must be considered. In swimming Chelonia the hind limbs move in more or less horizontal arcs when propelling the body through the water. In terrestrial forms the arc of movement can not be horizontal, for the foot has to be lifted off the ground to be placed in a forward position; the limb, then, must move in a more vertical arc. This fact causes the pelvic muscles to be arranged in such a manner that they produce a vertical pull upon the limb. The origin of the muscle must be, correspondingly, sufficiently far from its point of insertion to give the proper leverage during the act of moving the limb. The only way to create such an arrangement is to have the part of the girdle to which the muscles are attached raised above the area of the femur on

which the muscles are inserted. Hence the buckling of the ischio-pubic part of the girdle, with the result that it is raised to the level of the acetabulum.

6) KINOSTERNIDÆ

(Fig. 7)

This family is represented by species that are fundamentally palustral in their habits. The mode of life seems to be expressed in the nature of the lateral ischio-pubic arch, which is of a type intermediate between the kind found in *Testudo* and that associated with the more primitive *Pseudemys*. The only noteworthy feature of the pelvis is the widely flaring pectineal process of the pubis. The only other family of semi-aquatic Chelonia that shows this tendency is the Chelydridæ with which the Kinosternidæ are no doubt related through a common ancestor. In the Chelydridæ, however, the pectineal process is pulled well forward while in the Kinosternidæ it is extended laterally as a broad wing, making the whole girdle proportionately wider than the one found in the snappers. The difference in the form of the pectineal arch very possibly indicates that the musk turtles are somewhat more terrestrial than the Chelydridæ. The very small fenestræ between the pubis and ischium of the Kinosternid pelvis, combined with the extensive line of the symphysis between the two elements, are characters suggestive of the primitive Baenidæ and Pleurosternidæ from which the musk turtles seem to be an indirect offshoot.

7) CHELONIIDÆ

(Fig. 8)

In passing from the amphibious-terrestrial types of Cryptodira to the free-swimming ones, great changes in the pelvic structures must be expected. Three factors are directly responsible for such changes. Most important of these is the influence of the hydrostatic pressure upon the body, which buoys up the animal and relieves the pelvis of the concentrated body weight. Secondly, the liquid type of medium prescribes an entirely different movement of the limbs in locomotion from that possible in atmospheric surroundings. The hind limbs can be brought forward and pushed backward through horizontal arcs instead of vertical ones so characteristic of the land animals. Correspondingly, the musculature of the pelvis becomes flattened and broad to produce anterior-posterior pulls in planes very different from the planes used by terrestrial species. Thirdly, the shape of the body is changed, becoming more flattened dorso-

ventrally and tapering at the posterior end to produce a "run" that offers the least resistance in swimming and permits the ready flow of water over and off the posterior end of the body.

The influence of these three factors is seen in the following changes. The ischio-pubic arch has become widened out so that its lateral diameter is almost as great as its length. This change is due almost entirely to the expansion of the pectineal wings of the pubis, which, at the same time, are carried well forward. Thereby the lateral ischio-pubic arch becomes squat and wide to fit the pubo-ischio-femoralis-externus muscle, so constructed in these forms as to give a horizontal swing to the limb. In order to balance the lines of force in the forward-protruding pubis, the ilium becomes correspondingly tilted to the rear, now lying well behind the vertical norm. The equilibrant of the pubo-ischial forces lies somewhat tangential to the slightly curving ilium. In order to compensate for the peculiar position of the equilibrant, it becomes necessary to consider this line as a chord subtending an arc; then from the chord trusses may be constructed that will fit into the curved ilium and outline the course of the arc.

The parallelogram of the resolved forces becomes long and narrow in the case of the Cheloniidæ. The longer side indicates the greater reaction and represents a certain proportionate magnitude to the lesser force; the ratio of the magnitude of the forces acting through the pubis and ischium is not vastly different from the lines representing the directions of these forces. It is therefore possible to determine which of the several forces that are acting is the greater and to which member the force is applied.

In the Cheloniidæ there is no doubt as to the proportionate distribution of these forces. By a wide margin the maximum action passes through the axis of the pubis. Its smaller companion acting through the ischium represents a weaker component established when the main force from the ilium is broken up and distributed in the acetabulum.

The study of the relative lengths of the ilia of the Emydidæ, Kinosternidæ and other semi-terrestrial or terrestrial forms when compared with the Cheloniidæ is an interesting subject. In the former cases the ilium is by far the largest of the elements of the pelvis, being longest and heaviest in its build. In the latter case it is much the shortest and apparently weakest part, devoid of all excrescences that characterized the ilium in land-living Cryptodira. As the great body weight of the Cheloniidæ is considerably reduced by the hydrostatic effect of the environmental medium, which prescribes a swimming type of locomotion.

it is no longer necessary that the ilium be heavy and long, and provided with expanded surfaces for the attachments of over-developed walking muscles. The ilium is reduced to a secondary rank and in a sense replaced by an overgrown pubis that becomes the main place of attachment of the hypertrophied swimming muscles.

There is a striking resemblance in the pattern of the Cheloniid pelvis and that of a Chelydrid. The author is inclined to believe that the similarity is more than a mere parallelism due to more or less comparable environments. The two types of animals practice two different methods of swimming. The one (Cheloniid) never becomes terrestrial except during the short breeding season while the other is habitually amphibious. The structure of the hind limb and its skeletal framework in the Cheloniidæ is markedly different from the condition in the Chelydridæ. The body weight is carried in an entirely different way in each of the two cases. Yet there is a ready comparison to be made in the pelvic pattern of these two families, the one usually considered quite primitive while the other is acknowledged to be one of the most specialized of the Chelonia.

The same tendency in fenestration appears in both pelves, the Cheloniid carrying the process to a higher degree than any other Cryptodiran form. The retention of the pronounced elongated ischio-pubic ligament in the Cheloniidæ agrees with the presence of the same, but somewhat shorter and heavier, structure in the Chelydridæ. The gradual enlargement of the whole pubis (*cf.* section on Baenidæ-Chelydridæ) is a tendency marked by the expansion of the lateral wings of that member in the Chelydridæ and is comparable to the still greater expansion of them in the Cheloniidæ. While an expanded pubis is constantly associated with aquatic and swimming habits, there are several ways in which the increase in size might occur; the fact that the pubes of these two rather different chelonians possess modifications of the same kind may indicate that there is a close genetic relationship between them. It is entirely possible that each represents an independent line of descent from a common *Baena*-like ancestor.

8) TRIONYCHIDA

The same tendencies toward flattening of the body and expansion of the pelvis, as described for the Cheloniidæ, are present in the Trionychida, but these are carried to an even greater degree of development. This is especially evident in the construction of the pubo-ischial arch, which in this suborder is the widest and squatest of any found among

the Chelonia. The lines of force acting through the respective members of the arch intersect at a pronouncedly obtuse angle in the center of the acetabulum; the equilibrant of the force polygon appears much as it did in the case of the Cheloniidæ; that is to say, it represents a chord subtending a curved or arcuate ilium. The analysis of the equilibrant is made in the same way as in the preceding family.

By virtue of the extreme flattening of the body the pubes are prevented from buckling in both an antero-posterior and a right-left direction, and hence remain, in this suborder of turtles, as a pair of flat plates. As compensation for the inability to buckle, the pubes become very large in proportion to the other elements of the girdle, and are pulled well forward. In fact, their forward migration breaks down any remnant of a pubo-ischial ligament that may tend to form. The depressed body and the very flat pelvis may have some correlation with the peculiar self-burial habit that these species are prone to practice. They are able to work their bodies into the soft mud and silt of streams by a sidewise motion of the body accompanied by a twisting and undulating of the soft lateral edges of the leathery carapace.

The pronounced flaring of the lateral wings (pectineal processes) of the pubis represents an interesting parallelism between the Trionychida and the Cheloniidæ and Dermochelidæ. Only in *Dermochelys*, *Archelon* and *Protostega* are the pubic wings proportionately larger than in the Trionychida. It is important to note that forces acting through the central axes of the medial plate and the lateral wing of the pubis form the sides of a parallelogram, the equilibrant of which passes through the central axis of the proximal portion of the pubis, *i. e.* that portion which contributes to the formation of the anterior face of the acetabulum. The presence of this second polygon of forces acting solely within the body of the pubis is recognizable in all the other suborders and families of the Chelonia but is not so clearly marked nor so easy of analysis as in the Trionychida, Cheloniidæ or Dermochelidæ. The polygon represents the way in which the forces of internal stresses are resolved into lines of action so as to distribute the forces throughout the entire pelvis.

9) PLEURODIRA

(CHELYDIDÆ AND PELOMEDUSIDÆ)

(Fig. 3, Fig. 10)

The pelves of these Chelonia differ from those of the Cryptodira in being fused with the plastron. Therefore it is logical to expect certain

discrepancies in the general truss pattern to appear. The most marked of these is that each half of the pelvis is practically independent of the other half. The right pubis, ischium and ilium exist in such a state that the lines of symphysis between the two adjacent pubes and ischia are reduced to a minimum and in some instances practically do not occur at all. Any stress that one half might produce would not be taken up and affect the other; therefore even though one half of the pelvis should be damaged or disrupted in some way, the other half, being fused with the plastron, would be prevented from collapsing. The analysis of a Pleurodiran pelvis becomes simplified, for one is dealing with a single truss which bears practically no functional relationship to another truss. In fact, it was while studying the pelves of these Chelonians that the writer was impressed, for the first time, with the idea of a physical analogy between the pelvis and a simple truss.

When two bilaterally placed trusses mutually react upon each other, as is typical for the Trionychida, Cryptodira and Atheca, each becomes modified to accept the interaction. But in the case of the Pleurodira, where there is very little or no bilateral interaction, the respective bilateral trusses act as independent units; hence in the truss analogy the Pleurodiran pelvis can be expected to follow all the laws laid down for truss structure of the simplest type.

In order that the pelvis may be fused with the plastron, the pectineal process of each pubis becomes hypertrophied at the expense of the medial pubic plate, which in turn becomes much reduced. In like manner the medial arm of the ischium remains small while the ventral posterior process enlarges to form a broad articulating facet to fit into the plastron. The ilium is a very compact and broad member in the Pleurodiran pelvis and is placed in a more upright or vertical position than is the case in any other type of chelonian girdle, possibly excepting the one in *Triassochelys*. The compactness and solidity of the ilium give the observer the impression of an unnecessary resistant strength embodied in this member, for these animals apparently do not need powerfully built girdles, being mainly aquatic forms with sluggish immobile habits and only fair swimming ability. Few become terrestrial except for breeding purposes.

Although all Pleurodiran species are primarily aquatic, the one typical feature of the truss pattern correlated with this environment and so typical in other water-living Chelonians is not represented in the pelves of either the Chelydridæ or Pelomedusidæ. I refer to the nature of the lateral pubo-ischial arch, which in this suborder remains very high and narrow.

Perhaps the retention of the abnormally high arch accounts in some measure for the relatively poor swimming ability exhibited by these animals.

THE INTERNAL ARCHITECTURE OF THE PELVIS

THE ARRANGEMENT AND ANALYSIS OF THE TRABECULÆ OF THE ILIUM

Not only is it possible to make a physical analysis of the truss patterns of the chelonian pelvis, but it is possible also to study the finer build of the bone, make an analysis of it, and from the engineering point of view show the relationship between bone construction and external form. Before giving the details of the methods of observation and analysis it is necessary briefly to summarize the work done previously in this field and to lay down certain important engineering principles.

That bone acts in many respects like wood or metal has been proved by Rauber ('76), who demonstrated through experimentation that bone is an elastic material and therefore can be studied by the same analytical methods applicable to other elastic materials. In studying the finer structure of the pelvis, one must keep in mind that the elements making up the girdle are subject to at least three different types of stresses; these are compressions, tensions and shears.

According to the work of Koch ('17) and the earlier investigators bone is a fibrillated substance composed of Haversian systems, which are compacted into grosser threadlike units called trabeculæ or cancelli. These cancelli are so arranged in the bone that they represent, in their position, the lines of maximum stress throughout the various sections of the bone. As described in the historical résumé, two such sets of cancelli are found in the human femur; they represent the courses taken by the compressive and tensile stresses and are so termed in the literature of the subject.

By mathematical and mechanical computation Koch determined the exact position of maximal and minimal points of stress and found that these lie at very definite and respective points along the courses taken by the different tensile and compressive sets of trabeculæ, thereby emphasizing the fact that the trabeculæ represent the courses taken by the internal forces of the bone in resisting the external loads applied.

An analogous pattern of trabeculæ representing similar courses of compressive and tensile stress are to be found in bones other than human. While these trabeculæ are analogous, their positions vary a great deal by virtue of the differences in the modes of locomotion and in the resting positions of the different animals. The chelonian femur, for example, is not vertical in position as is the human but is held in a lateral or

dorso-lateral position, and during the act of walking swings in an arc that is more lateral than vertical. The body weight or external load thrust upon the chelonian femur produces a shearing stress of relatively greater magnitude than that produced in the human femur. Hence it must be expected that the cancelli arrange themselves in a different pattern to take up the relative increase in the shearing stress.

Likewise in the pelvis analogous stresses occur, but the forces, taking different lines of action, call for different patterns of arrangement of cancelli from those found in other bones of a vertebrate.

In an earlier section of this paper it was pointed out that two important loads are applied to the pelvis. One of these is a lateral thrust applied at the acetabulum, which is carried there by the body weight transmitted through the femur. The other is a load concentrated at the dorsal end of the ilium, carried there by the carapace and transmitted throughout the pelvis to the ventrally placed plastron. In the Cryptodira the second of the above loads causes the pelvis to be continually under compression while in the Pleurodira additional tensile stresses are present by virtue of the complete union of the plastron to the pubis and ischium.

The ilium in the Chelonia exists as a hollow column of bone. A thick outer wall surrounds a central cavity, which is provided with a spongy network of softer bone, extending the entire length of the cavity. At the proximal and distal ends of the ilium the compact outer wall merges with the looser central mass, so that at these extremities there appears a large mass of material, usually called the *substantia spongiosa*, which is neither so compact as the thick wall of the ilium nor so loose as the bone in the marrow cavity. In this respect the composition of the ilium is much like that described for the human femur, and its engineering and mathematical analysis is much the same.

In a hollow column the compact outer wall is the region where the tensile, compressive and shearing stresses occur. In a region where the wall is more or less uniform in diameter and thickness, these stresses proceed along more or less parallel paths; but in the upper and lower ends, where the *substantia spongiosa* appears, the lines of stress diverge from one another to distribute their actions throughout the mass of softer bone; yet the spongy bone must be so constructed as to offer the proper strength consistent with the use of as little organic material as possible.

According to the most elementary principles of mechanics, the most efficient way in which stresses are distributed is by the arrangement of resistant materials in the lines of, or parallel to, the courses taken by those stresses. It may be expected, therefore, that the bone in the ilium

will be of such a composition as to reflect the condition and the direction of the stresses which occur in it. It is found, indeed, that in the mid-portion of the ilium, where that element possesses its smallest cross-section, the stresses are so close together that the cancelli in the bone must be very compacted. At the proximal and the distal ends of the bone the cancelli diverge into a fanlike pattern conforming to the lines taken by the stresses in these regions.

The ilium acts as a vertical column or a beam and as such conforms to the general laws underlying the composition of mechanical beams and columns. A survey of a few of these laws is necessary before an attempt is made to give a detailed description of the composition of the ilium.

LAWS OF BEAMS AND COLUMNS

If any beam is studied carefully from the point of view of the mechanical and physical laws that govern its make-up, it is found that the beam is made of resistant fibers arranged in more or less parallel courses and that these fibers resolve themselves into two groups: those that resist vertical stresses and those that resist horizontal stresses. The ones that resist the vertical stresses are the shearing fibers while those that resist the horizontal stresses are the compressive and tensile fibers. Assuming that the beam is placed in an horizontal position and is sustained by one or more supports, it will be noted that there is a constant tendency for the beam to bend, due to the weight of the beam itself and to the application of any load at any point along its course. The result is that complex stresses and elastic deformations are produced. These can be resolved into various stresses of tension, shear and compression. When certain data are known, the amount of stress in any cross-section of the beam may be determined and can be graphically represented.

The tendency of a beam to rotate about its point of support is measurable, and is determined by calculating the bending moment of the beam; such a bending moment at the point of support is found to be the product of the load, multiplied by the distance of the load from the point of support. If x (Fig. 11) indicates the distance of the load L from the point of support $Ps.$, then the bending moment of the beam is expressed as $Mb. = L \cdot x$. This formula would hold true only in the analysis of a cantilever beam, i. e., a beam in which the point of support is at one end only. A similar formula can be worked out for a beam with two supports. In order to determine the bending moment at any or all points along the beam, the formula $Mbx, x_1, x_2, x_3 \dots x_n = Lx, Lx_1, Lx_2, Lx_3 \dots Lx_n$, may be applied. The bending moments of a horizontal cantilever beam

may be graphically represented by scaling the coordinates upon a base line drawn parallel to the beam (Fig. 11).

A vertical shear in a beam is caused by two parallel and equal forces acting in opposite directions in the vicinity of the one section. In a cantilever beam the vertical shear is uniform throughout the length of the beam, assuming the latter to have a uniform cross-section. Like the bending moment the vertical shear may be graphically represented (Fig. 11).

When external forces act upon a beam, they are counterbalanced by internal stresses (forces), which keep the beam in equilibrium and cause it to maintain its integrity. In any section of a beam the external forces tend to disturb the equilibrium, and to the engineer the main problem in the study of a beam is to determine the nature and magnitude of the internal stresses which prevent deformation of the beam. Upon making a careful analysis of his problem, an investigator finds that in all beams there are two types of stresses which counteract the external forces. These are tensile and compressive stresses. After making his calculations he comes to the conclusion that:

The sum of all the vertical forces $= 0$

The sum of all the horizontal forces $= 0$

The sum of the moments of all forces $= 0$

The sum of all the horizontal stresses $= 0$

The sum of all the compressive stresses $=$ the sum of all the tensile stresses.

The detailed proof of these very fundamental laws of mechanics would take up too much space in this paper and would not contribute anything new to knowledge. It will be necessary, therefore, to accept these laws in a more or less axiomatic way and the reader is referred to the numerous books on mechanics and dynamics which treat the solution and proof of them in detail.

A few other principles governing the action of beams must be considered at this point. When a beam bends, one side of it becomes convex and the other concave; the elastic fibers that make up the beam elongate on the convex side and shorten on the concave. It is readily seen that the elongating fibers are the tensile ones and the shortening fibers the compressive. By experiment it can be shown that there is a central portion of the beam in which the fibers are neither shortened nor elongated. The area so constituted is called the *neutral surface* or *neutral axis* (Fig. 12). After a series of observations on the change in shape and length of the

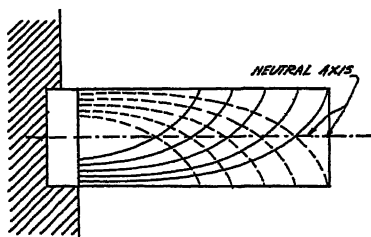
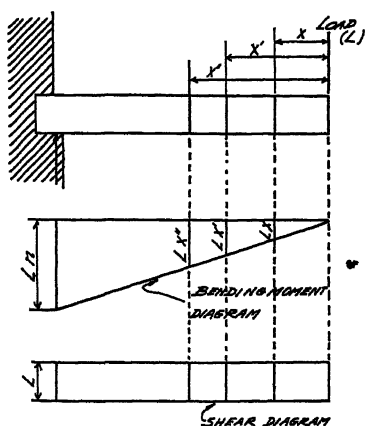
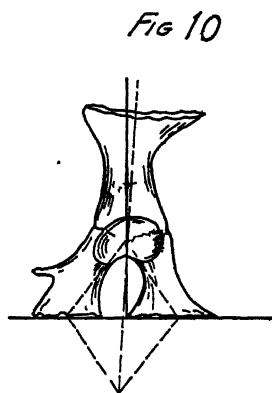
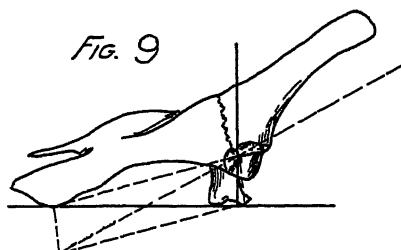
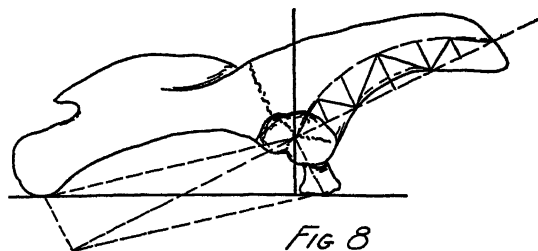


FIG. 8.—Pelvis of *Chelone mydas* with the analysis of the ilium in the form of an arch, the chord of which represents the equilibrant of the lines of force in the pubis and ischium.

FIG. 9.—Pelvis of *Dermochelys coriacea* to illustrate the most extreme type of pelvis in which the equilibrant does not pass through a main part of the ilium.

FIG. 10.—Pelvis of *Chelys ambrata*, which illustrates the simplest type of truss construction in the Chelonian pelvis. This form is representative of all the Pleurodira.

FIG. 11.—A beam of the cantilever type with the diagrams of the bending moment and shearing moment graphically shown. For the details of this analysis the reader is referred to any of the standard books on structural design.

FIG. 12.—The typical paths of stresses occurring in a beam which has approximately the same overhang and stress relations as the ilium of *Testudo*.

internal fibers one comes to the following conclusions regarding their behavior:—

- a) The change in length of a fiber is directly proportional to its distance from the neutral axis.
- b) The stresses carried by the horizontal fibers are directly proportional to their distances from the neutral axis, provided, of course, that the unit stresses are less than the elastic limit of the material that makes up the beam, and prevent rupture.
- c) The neutral axis passes through the centers of gravity of all the cross-sections of the beam.

While the study of stresses in beams and their organic counterparts in an animal body are very important in a mechanical interpretation of the skeleton, the laws underlying the composition of columns is likewise vital. Many of the laws applicable to the theory of beams are likewise applicable to the theory of columns; yet there are certain additional remarks that must be made.

The value of a column depends upon certain very definite factors. The material of which it is constructed is more or less dependent upon a) the cross-sectional area, b) the cross-sectional shape and c) the proportion between the area of the smallest cross-section and the total length of the column. By changing the ratio between the least cross-sectional area and the length of the column the rigidity and the supporting value of the column become changed, unless the material of which the column is made is replaced by a more resistant one, or unless the cross-sectional shape is altered. All these factors are to some degree interdependent, yet each carries a value all its own.

DETERMINATION OF THE NEUTRAL AXIS OF THE ILIUM

The ilium, as previously stated, represents a hollow column. Although not so perfect a replica of such a column as that constituted by the human femur, yet the analogy is quite clearly seen if either cross-sections or vertical sections of the ilium be made (Fig. 13A, and Plates IV and VII). With careful observation the following facts can be determined. The outer wall of the ilium is not uniform in thickness over the entire surface of the bone. At the proximal and distal thirds of the element the wall consists of a fairly thin, homogeneous bone, which at the very extremities (dorsal and ventral) becomes rather cancellated. In the middle third of the column, *i. e.*, the area of least cross-section, the column has been reinforced by the production of a very thick and compact wall of bone, which graduates with the thinner lamellæ of

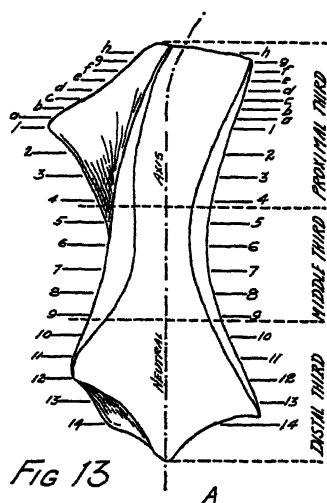


Fig 13

A

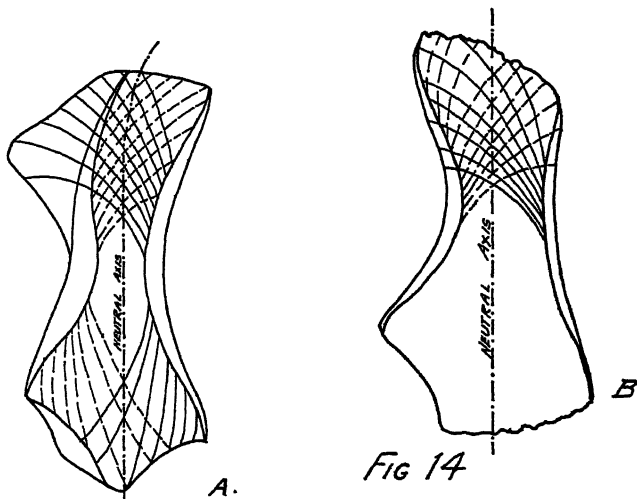


Fig 14

FIG. 13.—Diagram of the frontal section of the ilium of *Testudo* to illustrate a hollow column. Lines *a* to *h* and 1 to 14 indicate the sections cut in the determination of the neutral axis.

FIG. 14A.—The paths of stress in the upper and lower ends of the ilium of *Testudo*. Compare with the illustration of the cancelli in this animal and the figure of the lines of stress in a beam (Fig. 12).

FIG. 14B.—The lines of stress in the proximal end of the ilium of *Chelone*. Compare with Figs. 12, 14A and the photograph of the ilium of *Chelone* in frontal section.

the two distal ends. Unlike a mechanically constructed beam or column, the ilium is not uniform in its cross-section. The area of least cross-section is somewhere near the mid-point between the upper and lower ends, though it does not necessarily coincide with that point. As one passes away from the area of least cross-section, the ilium widens considerably and rather rapidly and as a result both the sacral portion and the acetabular portion are greatly distended, imparting what might be termed an hour-glass form to the whole element (Fig. 13). Due to this external form and exaggerated by the appearance of a very thick wall in the middle of the ilium, the cavity of the bone assumes a narrow mid-section and wide flaring extremities. Due to the shortness of the whole ilium, the cavity in it is not so pronounced as that found in a longer bone like the femur; however, one can easily recognize that in the mid-portion of the ilium the bone is much looser and more spongy than at either extremity. The cavity itself is rather short, for the upper and lower ends of the element must be so constructed as to provide for the cancelli that are to carry the various stresses through them.

As mentioned above, in describing the theory of columns and beams, it is very necessary to determine in any column or beam the neutral axis, which represents the line through which there is neither elongation nor foreshortening of the fibers that make up the beam or column. In the usual types of columns and beams used in mechanical construction the neutral axis coincides with the structural center of the appliance. In such a natural column as a human femur or a chelonian ilium the neutral axis may conform to the morphological center or it may not, depending upon the position and the courses taken by the various stresses within the bony element. The neutral axis cannot be drawn, therefore, merely as a line passing through the mid-points of the various sections of the bone. Under the laws of beams it was ascertained that the neutral axis always coincides with the centers of gravity of the various sections of the beam. The same is true of a column and it becomes necessary, therefore, to determine first the centers of gravity of the various cross-sections into which a chelonian ilium may be cut. In order to do this the ilium is fastened into a small miter box and with a jeweler's saw cross-sections are cut in series so that each section is as thick as an ordinary lantern-slide cover glass. By the simple method of suspension the center of gravity is determined for each section. Then a very careful outline of the cross-section is traced upon a previously prepared cover glass. The glass is thoroughly cleaned and a very thin

solution of gum damar in toluol is allowed to run over the surface; the glass is set aside to dry for a short time. In this way the glass with its damar surface will "take" India ink. When all the sections have been traced, one on each slide, the slides are stacked up in the order of the serial sections. The points of the centers of gravity having been indicated on the tracing, it is a very easy matter to see the continuity of these points through the layers of glass. It can be determined now whether the line connecting the centers of gravity (the neutral axis) is a straight line, a zig-zag or a curved line. With this model in front of the observer, the position of the various cancelli are studied and their respective distances from the neutral axis are determined, for according to the elements of mechanics it is important to know how far a stress-bearing fiber diverges from the neutral axis in order to calculate its mathematical value.

THE ILIUM AS A COLUMN: EXTERNAL ASPECT

Very few of the chelonian ilia are in the form of cylindrical equisectional columns. Most of them are hour-glass shaped with extremities that are knoblike or provided with wide flaring wings. At the distal end there are three prominent facets, which articulate respectively with the ischium, pubis and femur. Proximally there is the surface for articulation with the sacral ribs but in many forms additional surface is provided for attachment to the carapace. As described in the section on truss analogies, it is apparent that two distinct lines of action pass through the ilium. One of these reaches from the sacral region to the distal end and there divides so that its components pass, with proportionate magnitudes, through the pubis and ischium. The other extends from the sacral region to the acetabular facet, there to be transferred to the femur and thence to the lower leg. Therefore, it must be expected that two very distinct sets of stresses occur and that the cancellation of the bone will follow the pattern laid down by these stresses.

In observing the surface of the ilium, it is quite apparent that the cancelli are not restricted to the inner composition of the bone but extend all the way to the superficial wall and show through as delicate striations, extending along the long axis of the element. Depending upon the shape of the ilium, these striations will be more or less spirally arranged around the surface.

In all the specimens examined the two sets of surficial cancelli take the following courses. The one set, arising in the ectal edge of the

proximal part of the ilium, passes obliquely around the posterior face of the bone and finally reaches the distal inner (mesal) surface; there it spreads out to distribute the superficial stresses to the pubic and ischial facets of the ilium. The other set, arising at the sacral facet of the ilium, passes from that area, which is on the mesal-proximal region, to the ectal-distal end of the bone, there to terminate in the acetabular facet.

The more cylindrical the ilium is, the less evident is the spiral pattern of these cancelli, while it becomes more and more pronounced as the ilia assume an hour-glass shape and are somewhat flattened. The paths of the cancelli as they cross one another represent the two sets of internal forces at work, the compressive and the tensile stresses, which are so arranged as to maintain a static condition in the bone and prevent distortion or deformation of it when the various external forces play their respective rôles. The main thrust of the body weight upon the femur indicates that the cancelli arising at the inner sacral facet and passing to the outer distal end of the ilium are compressive ones and are continually resisting the load applied at the proximal end of the bone, thus preventing the dorsal and ventral planes of the body from being squeezed together. Likewise the cancelli extending from the outer proximal end to the inner distal end of the ilium represent the tensile group and prevent the various parts of the bone from pulling apart.

THE ILIUM AS A COLUMN: INTERNAL ASPECT

(Figs. 14A and B and Plates IV, V, VI)

As previously stated, when the ilium is sectioned either in transverse planes or in a vertical one, it is very clearly seen that the form of the bone assumes the construction of a hollow column. From the point of view of elementary mechanics this specific condition provides for the maximum resistant strength with the expenditure of the least amount of material. The rigidity and the moment of inertia of the column depend, of course, upon the area of least cross-section, which in the ilium of the turtles is somewhere near the mid-point of the longitudinal axis of the bone. A certain factor of safety is established by the fact that the wall of the ilium in this region is considerably thickened to prevent lateral shearing stresses from exceeding the elastic limit of the bone.

The indications of the stresses, as seen on the surface of the ilium, become very clearly marked in the internal composition of the bone. The cancelli appear as very delicate tracings in the substantia spongiosa

while in the area of least cross-section they are so close together that they form an indistinguishable mass of compact bone. Basing the study of these cancelli upon the already established premise that the lines of stresses in any body are represented by the appearance of resistant material either directly in the line of stress or parallel to it, it seems definitely certain, then, that the cancelli indicate the lines of action of the internal forces and that their positions should follow the courses taken by the various stresses. This conclusion is emphasized by the fact that, when the position of the cancelli is studied in relation to the line joining the centers of gravity of various and all sections of the ilium, it is found that none of the cancelli coincides with that line, which represents the neutral axis through which no stresses pass.

In all the material examined the pattern of the internal cancelli seems to be rather constant. Of course there is a certain variation in the position of these delicate strands of bone in the different ilia, but these minor variations are due primarily to the different weights of the body and the somewhat different position of the animal during its resting attitude. The general pattern seems to be constant, however, and can be described for one species as representative of the rest. For this purpose *Testudo pardalis* has been selected, for it shows most clearly the position of the trabeculae. In order to compare such a purely terrestrial form with other types of Chelonia, a brief description of *Chelone* will be given presently, since that animal represents the opposite extreme of habitus characters.

THE INTERNAL CANCELLI OF THE ILIUM

(Figs. 14A and B, and Plates IV and V)

By making very thin sections of the bones studied, the position of the various cancelli within the bone may be readily seen. The sections are cut with a very fine jeweler's saw, as previously stated, to about one millimeter in thickness; frontal sections are cut whenever possible so as to give the maximum extent of the courses of the cancelli as they pass from the distal to the proximal part of the ilium. Much as in the figures published by Koch ('17) to illustrate the composition of the human femur, the cancelli in the chelonian ilium form two distinct groups, which extend more or less vertically through the ilium from the distal to the proximal end and which arise respectively from the ectal and ental portions of the column. These two sets of cancelli represent the compressive and tensile resistant material within the bone.

For convenience of description the ilium may be divided into three morphological regions: the distal part represents the area adjacent to the articular facets of the ischium, pubis and acetabulum; the middle third represents the area of the least cross-section and its adjacent regions, while the proximal portion represents the regions adjacent to the articular facets for the sacrum and carapace (Fig. 13A).

CANCELLI OF THE DISTAL PORTIONS

Several sets of rather confusingly arranged trabeculae occur in this region. In the sectional views (Plate IV) two articular facets are seen with their spongy bone radiating respectively ectally and entally from their surfaces. Those cancelli arising from the acetabular facet represent the compressive stresses (ectal series) while those arising from the ischiac facet are the tensile trabeculae (ental series).

A) Ectal series:—While the cancelli of the ectal series primarily represent the compressive group, there is some indication that intermingled with them are smaller and less distinct cancellations, which probably represent tensile stresses in this region. The primary ectal series, however, is very distinct and takes on the following form. Extending from the acetabular facet these cancelli pass ectally somewhat obliquely to fuse with the lower limit of the very thickened wall of the ilium in its middle-third region. While these longitudinal cancelli are sharply defined, they are compacted and in all instances provided with short transverse stout bony fibers, which appear to be usually at right angles to the main axis of each pair of cancelli. These transverse fibers must act as reinforcing strands, for they give a very positive reticulate appearance to the substantia spongiosa in this region, making it look more solid here than at any other portion of the ilium. While the compressive cancelli extend from the acetabular surface to the ectal wall of the column, they do not do so in parallel lines but in convergent fashion. The result is that the intervals between the individual fibers on the ectal wall of the ilium are smaller than the intervals between the same fibers on the acetabular facet. By the time the fibers have reached the wall of the column they lose their identity and become so compacted that they form one solid mass in the ectal wall. The reason for the pronounced compacting of the cancelli in the ectal series at the distal end of the ilium is probably that this is the region of greatest thrust from the femur, the entire body weight being carried upon this small area through the acetabular facet.

The less distinct, probably tensile cancelli of the ectal series appear as delicate fibers arising from the very distal extremity of the acetabular region and extending to the ental wall of the column just above the ischiac facet. Like the compressive cancelli above described, the secondary series are radiating fibers between which appear small bridge-like cross-bars that are probably reinforcing strands. This secondary series of fibers fans out to occupy the entire ental region of the distal third of the ilium.

B) Ental series:—While not so extensive as the ectal series, the tensile cancelli of the ental series are no less distinct. Like the compressive fibers of the ectal series these analogous ones arise from the ischiac facet and extend in a convergent fashion to the ental wall of the iliac column, there to fuse indistinguishably with the bone of the wall. Incidentally these fibers cross at about right angles the more delicate, apparently tensile fibers of the ectal series.

In the arrangement above described, the animal has undoubtedly constructed the bony part of its ilium in such a manner as to meet the particular demand set upon this portion of the element; just as ectal tensile and ental tensile cancelli are arranged in the acetabular-ischiac region, so similar ones appear in the acetabular-pubic region, the tensile fibers of the pubic section converging with those of the ental wall around the ischiac portion. These relationships cannot be seen in the figures shown, for the sections represented do not pass through the pubic facet; one would have to cut other sections sagittal or sub-sagittal, as the case may require.

CANCELLI OF THE MIDDLE THIRD

The cancelli described for the distal portion of the femur converge from that more or less dilated region to the narrower middle region, which represents the area of least cross-section and the adjacent portions of the column. In about the middle third of the ilium the ectal and ental walls become very thickened, the ectal wall, which bears the compressive cancelli, being about twice as heavily constructed as the ental wall, which bears the tensile trabeculae. Although the cancelli from both surfaces of the column unite with the bony wall proper and lose their identity for the greater part of their courses through this region, there is still a faint indication of the path taken by them. The inner surfaces of both the ectal and ental walls are not perfectly smooth but appear as pitted linings of the hollow iliac column. These pittings are due to the failure of the cancelli, which make up the greater part of the wall,

completely to coalesce. On the distal end of the middle third of the column, the cancelli from the acetabular and ischiac regions can be clearly seen passing into the ectal and ental walls; on the proximal end of the third of the column homologous cancelli can be seen leaving the walls and passing to the inner or outer sides of the proximal end of the ilium. By carefully tracing the positions of the porosities in the thick wall on the middle region the paths of the various cancelli can be followed from the distal to the proximal thirds of the whole column.

The neutral axis of the column passes approximately through the middle of the area of least cross-section. As was stated previously, the stresses carried by any resistant material of a column or beam vary directly as the distance of that material from the neutral axis of the column or the beam. In the area of least cross-section of a hollow column, represented by the ilium, the stresses are the greatest that occur anywhere in the column. Hence, the resistant material should be compacted in an area where the stresses are farthest from the neutral axis, and where the unit stresses will approach the elastic limit of the material making up the column. It seems obvious, then, that the area of least cross-section, which is the portion that takes up the brunt of the stresses of the entire column, should be the most compactly arranged and offer the greatest resistance to the internal forces acting in the column.

CANCELLI OF THE PROXIMAL PORTION

When the cancelli, so compacted in the middle third of the column, leave the ectal and ental walls respectively, they shape their courses in such a manner that the fibers originally on the ectal wall eventually terminate on the proximal ental wall and those arising from the ental wall pass to the proximal ectal portion of the column. By so doing they must of necessity cross over one another. Nothing more clearly represents the paths of tensile and compressive stresses in a beam than the arrangement of these cancelli in the proximal portion of the column. In comparing the figure of the frontal section of the bone with the diagram of the analysis of a hypothetical beam, one is at once struck by the similarity of the stress patterns. In the beam the two sets of stresses, compressive and tensile, form a rather symmetrical pattern, which is quite analogous with the somewhat more asymmetrical pattern formed by the cancelli in the ilium. In each case the path of the individual stresses figured is curved and the points of intersection of the respectively homologous tensile and compressive stresses lie in the neutral axis;

in one instance the neutral axis is a straight line, in the other instance slightly curved. The upper half of the ilium can be considered comparable to a cantilever beam, or the entire bone may be regarded as equivalent to a beam or column with two supports.

COMPARISONS WITH OTHER TYPES OF ILIA

The type of cancellation of the ilium as described for the genus *Testudo*, while typical, for the purely terrestrial Chelonian, is not limited to that major group of animals, but occurs also in other representatives. For the most part the ilia are small bones in the lesser forms of this order and show the cancellation pattern but poorly. When the ilium is more cylindrical than the type found in *Testudo*, which is distinctly of the hour-glass form, the cancelli extend lengthwise throughout the bone in a design more symmetrical than that characterizing *Testudo*, while in those ilia that are still more hour-glass shaped (*Chelys*, for example), analogous cancelli are more irregularly placed.

In order to compare the cancellation of the bone of a terrestrial tortoise with that of a chelonian of opposite habitus characters, a brief description of the ilium of *Chelone* is here given:—

The principal difference in the pattern of the ilium of *Chelone*, as compared with that of *Testudo*, is the absence in the former of the flaring head at the proximal and ental portion which so markedly characterizes the latter. As a consequence the upper end of the neutral axis passing through the ilium is turned somewhat ectally in *Testudo*, while it passes more vertically in *Chelone*. In spite of this difference in external appearance, the internal cancellation of the ilium from *Chelone* is quite like that of the ilium from *Testudo*, with a slight modification in the proximal portion, where the cancellation must conform to the position of the neutral axis. On the whole the make-up of the ilium of *Chelone* consists of a good deal more of the substantia spongiosa than is the case in *Testudo*. This fact gives a totally different appearance to the sections of the bone. Yet it is very evident after careful study that the bony fibers are arranged in *Chelone* in much the same manner as they are in *Testudo*, so that at the distal third of the ilium there are the two sets, ectal and ental cancelli, which again represent the respective compressive and tensile lines of stress. The middle third has the same thickened walls, but these are proportionally weaker than in *Testudo*, for in its aquatic habitat, the body weight of *Chelone* is buoyed up by the surrounding water and the factor of shearing safety employed in the area

of least cross-section need not be so great as that used in a terrestrial animal, in which the major part of the body weight is carried by the ilium. The proximal third of the ilium possesses both the compressive and tensile fibers described for *Testudo*, but the compressive ones are somewhat foreshortened, due to the fact that *Chelone* lacks the flaring ental head.

The constancy in the pattern of the internal cancellation of the ilia of the different habitat types seems irreconcilable, at first, with the difference in the general morphology of the same types as pointed out in that section of this paper dealing with the truss analogies of the pelvis. The very vertically placed ilium of *Testudo* in contrast with the much inclined ilium of *Chelone* or *Dermochelys*, suggests that the internal construction of the bone should be different in the two cases. Yet when the movement of the limbs and the position of the animal at rest is considered, it is apparent that the two habitat extremes have ilia that take up the external forces in the same or very much the same way and that the responsive growth of the bone of the ilium follows the demands of the forces applied externally to that element. In the terrestrial forms the principal thrust upon the ilium is carried vertically through the femur, while in the swimming types it is carried more horizontally, due to the antero-posterior movement of the limbs.

THE GRAPHIC ANALYSIS OF THE CANCELLI OF THE ILIUM

By first determining the centers of gravity of the various sections of one ilium, the respective points are plotted upon the figure of the opposite bone, and the line drawn between these points represents the neutral axis of that bone. Assuming that the two ilia are symmetrical, their neutral axes will be isomeric. When once the neutral axis is determined, points along its course represent regions where the compressive and tensile stresses cross and neutralize one another, with the result that at these points there will be no stress at all. If we bear in mind one of the most basic principles of mechanics, that the paths of stresses through elastic materials are outlined by the accumulation of resistant material so that there will be a maximum of resistant strength offered with the expenditure of the minimum amount of material, the plotting of the lines of stress in the femur can be undertaken. A strict mathematical determination cannot be made, due to the fact that certain important data are unknown, such as the live weight of the organism, the distribution of the weight on the four legs, which may possibly be

unequal, and the elastic limit of the bone. The last item could be determined experimentally if enough material could be secured; but with a limited supply of specimens this item has to be discarded. It is assumed in this paper that the elastic limit of turtle bone is very near that of the bone of other vertebrate animals, in which the ultimate strength ranges from 13,000 to 24,000 pounds per square inch, the lower limit representing tensile strength, the upper limit compressive.

In Fig. 14A is diagrammed the graphical outline of the cancelli shown in Plate IV. It will be seen that the lines representing the cancelli and therefore the stresses are arcuate and fall into two groups, the compressive and tensile. These are analogous to the similar line of stress that can be determined for a beam of two supports or, if attention is restricted to the upper half of the diagram, the pattern of the lines suggests the stress analysis of a cantilever beam (Fig. 12B).

DISCUSSION

It appears from the considerable amount of work done on the analysis of the bone, especially bone of the human being, that the construction of this tissue follows the influence of forces acting upon whatever member is studied. Bone acts, then, much as steel or wood does, in that in its own make-up it receives certain loads from external sources and tends to resist such forces as efficiently as possible. As a result the bone does not become a homogeneous substance but takes on a reticulate appearance, which has given the name *substantia spongiosa* to the less compact part of it. In this way the organism is able to offer the maximum resistant value with the use of as little bulky material as necessary, the organic material used being restricted to the regions where the internal forces at work in the bone are producing the greatest strain while they are off-setting the external stresses being applied to it.

In the first portion of this paper the writer described the construction of the pelvis as a whole and pointed out the great similarity that exists between that girdle and a mechanical truss. Just as trusses vary with the loads that they carry and the particular structures they are to hold up, so the pelvis in different *Chelonia* vary, for they are performing somewhat varied functions, dependent upon the habitat of the animal and the method of locomotion employed in the different habitats. The change in the relative sizes of the pubis and the ischium well illustrates the change in thrusts upon the pelvis. This fact coupled with the changes in position of the ilium in the respective cases heightens

the belief that there is an organic response to the external forces at work. The movement of the hind limb in a more or less vertical arc calls for a more erect and taller pelvis, while the movement of that limb in a more horizontal plane causes the pelvis to respond to that demand and the girdle becomes considerably inclined (to the posterior). This becomes apparent when *Testudo* and *Chelone* are compared. Yet in each case the mechanical ratios between the elements are kept constant, so that the lines of force acting through them will not be distorted and a state of equilibrium remains. This is accomplished, as has been pointed out, by varying the lateral ventral arch and the lengths of the pubis and ischium. While these proportions are kept more or less constant, the forces acting through the respective members are proportionally distributed.

In spite of the fact that great variation exists in the gross pattern of the chelonian pelvis, the finer structure of its bones remains fairly constant. This seems to suggest that it is easier to change the relative position of parts of a complex series of osseous elements than it is to rearrange the finer parts and the smaller units that make up the elements. Moreover, when once a bony element is in the form of a beam or column, the internal stresses remain rather constant regardless of what position that bone may occupy in the body, for although the external forces may be applied from different sources, the types of external forces are always constant, and the internal forces would naturally fall into a compressive series and a tensile series, constant in their nature, though not necessarily in their magnitudes.

When any mechanical object is subjected to external forces, the internal response of that object is the same irrespective of the material used in the composition of the object, so long as the internal response is below the limit of elasticity or breaking limit of the substance used. A wooden beam has the same reaction as one of steel so long as the internal stresses are not too great to produce distortion and subsequent rupture of the beam. It is true, of course, that a steel beam could be of much smaller cross-section since the finer material that composes it is more resistant or less elastic than wood, but the internal reactions in the two cases would be identical. It is not to be expected, therefore, that the bones of two animals will vary in their reactions any more than wood or steel, especially when it is considered that the bones in question are homologous structures and subjected to analogous forces both external and internal.

As has been pointed out by Koch, human bone (femur) has certain factors of safety commensurate with the actions in running, walking and standing. Although the factor of safety in the Chelonian pelvis has not been determined, it is very evident that one exists and that it certainly is not less than 5.0 (the minimum in the human); the pelvic elements do not reach the limit of elasticity by a great margin.

One of the most interesting features of the finer architecture of the pelvis is the intimate way in which the cancelli or bundles of cancelli extend from one element to another and dovetail the two or more pieces together. This is well illustrated in *Chelys*, where the girdle spans the interval between the carapace and plastron and is fused with each, to act as a composite column between a floor and a roof. In this case the sutures between the pubis, ilium and ischium are very deeply cut and, when these parts are disarticulated, it is found that prominent splinters of bone, which prove to be bundles of cancelli continuous with the ones in the elements themselves, force their way from one part to the other and hold the elements together. By itself, this fact is not surprising, but it is of great importance in the light of the function of the cancelli, and we must conclude from this fact that the various internal stresses are carried from part to part by these bundles of cancelli, which, when they reach their limits, transfer the stresses to other cancelli in the element into which they extend. By this marvelous mechanism the entire girdle becomes one continuous meshwork of cancelli in which each fiber is dependent upon every other fiber. It is still more remarkable when it is considered that the cancelli are arranged in a pattern that is to occupy the minimum amount of space and give the maximum resistant strength to the object which they constitute. In forms where the resistant shearing value of the pelvis must be great, the intergrowth of the sutures is most prominent. *Chelys* exhibits just such a case. The lines of union between the elements are prominent about the region of the acetabulum, the carapace and plastron. But in the region of the two opposite pubes and ischia there is no such interlacing of cancelli, for the preponderant stresses are not applied transversely across the body but are restricted to a more vertical course. In other forms, such as *Testudo*, where the opposite pubes and ischia abut, there is some indication of intergrowth of cancelli between the two elements. A similar condition is met with in those species of Chelonia, in which the pelvis is well arched and has passed out of the "plate" stage. In these instances there is a pronounced stress occurring transversely across the two halves of the girdle, since there is no fusion between the girdle and the plastron.

That the gross form of bone is dependent upon the finer architecture of it has been the deduction of many of the earlier workers—Wyman, Koch, Culman and others. In a like manner the present writer is of the opinion that the form of the pelvis is an expression of the arrangement of its cancelli, that these are the ultimate units that must be studied in making any analysis of the evolutionary history of the girdle and that until this is successfully accomplished, there can be no complete interpretation of the correlation between form and function.

CONCLUSIONS

It will be best to treat the foregoing paper in two sections, one dealing with the truss analogies and the other dealing with the conclusion arrived at from the study of the finer anatomy of the bony elements.

A) TRUSS ANALOGIES

The Chelonian pelvis represents a truss of a modified "king-post" type, which is described as belonging to trusses of the second order.

As a truss the pelvis falls under the influence of external forces such as affect a mechanical structure.

Three types of pelvic trusses are found. These are determined by placing the pelvis in a standard aspect for analysis, after which it can be seen that: a) *Triassochelys* represents the first group in which a vertical norm passes posteriorly to the ilium; b) the Baenidæ (in part) and Pleurodira belong to a second group in which the vertical norm passes through the greater part of the ilium; c) most of the modern species belong to a third group in which the vertical norm passes anteriorly to the ilium.

Lines of force acting through the pubis and ischium form the sides of a parallelogram of forces, the equilibrant of which extends through the neutral axis (center of gravity) of the ilium. In some instances the ilium is so curved (*Trionychoidea*) that the neutral axis does not coincide with the equilibrant, but forms an arc, the chord of which is equivalent to the equilibrant.

The more terrestrial forms possess pubes and ischia whose lines of force form a narrowed vertical parallelogram, the more aquatic types possess ischia and pubes whose lines of force form a more squat horizontal parallelogram.

B) FINER STRUCTURE OF THE BONE

The bone of the pelvis of the *Chelonia* is cancellated much as has previously been described for human bone.

The arrangement of the cancelli follows the courses of the internal forces in the bone and therefore the cancelli can be assigned to tensile and compressive groups, comparable to the tensile and compressive stresses in the bone.

The ilium (upon which the most work has been done) represents a column, hollow, with a mass of *substantia spongiosa* well defined at both the proximal and distal ends. The spongy nature of this part of the bone is due to the presence of cancelli, the ectal series of which are compressive, the ental series being tensile.

The construction of the bone conforms to the laws laid down by earlier workers for the human femur, in that there is the greatest resistant value assumed with the expenditure of the minimum amount of organic material employed.

The cancellation of the bones of the pelvis remains more or less constant although the gross pattern of the pelvis is varied in the different families of the *Chelonia*.

That the cancelli are the ultimate units of bone mechanics must be accepted and the analysis of their arrangement gives a mechanical interpretation of the gross anatomy.

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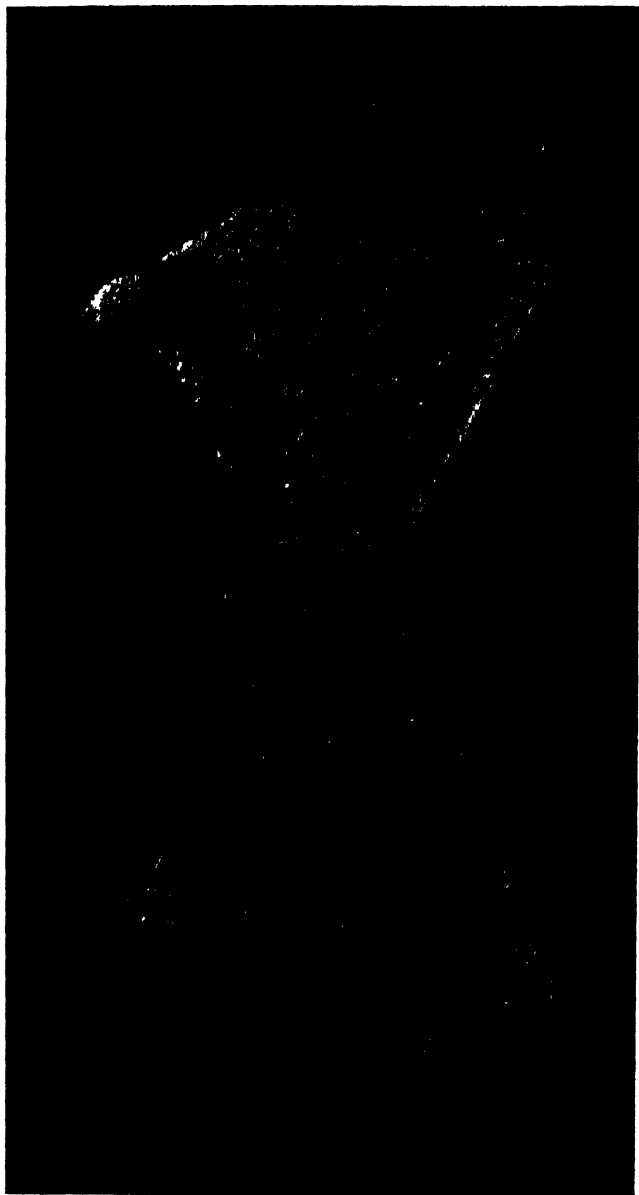
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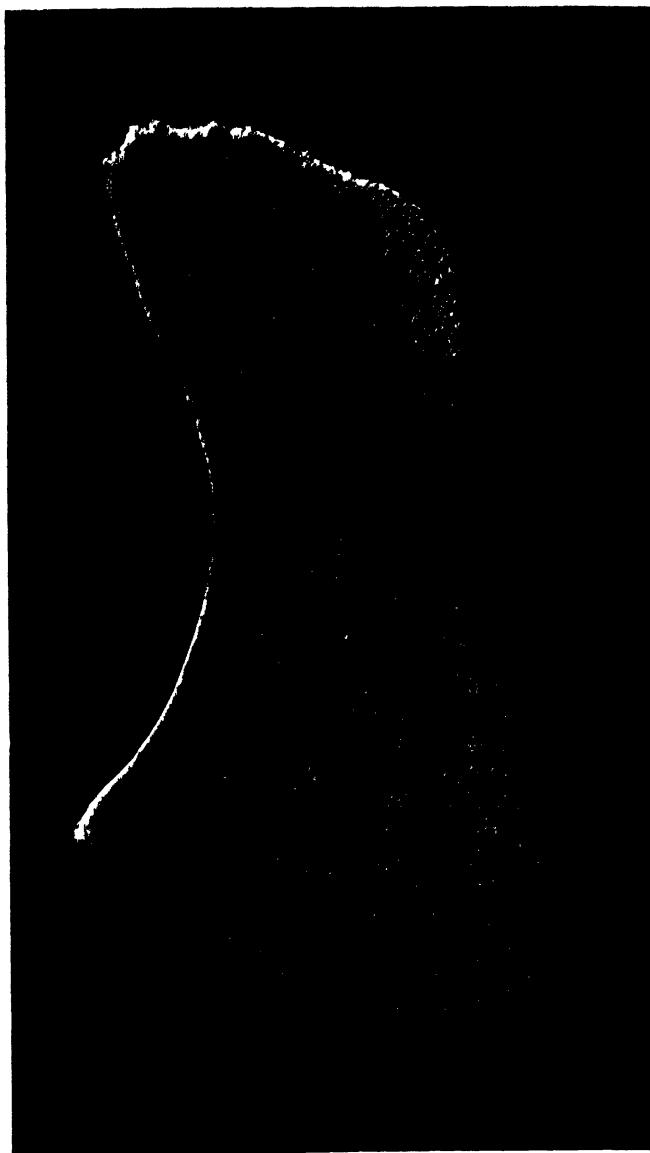
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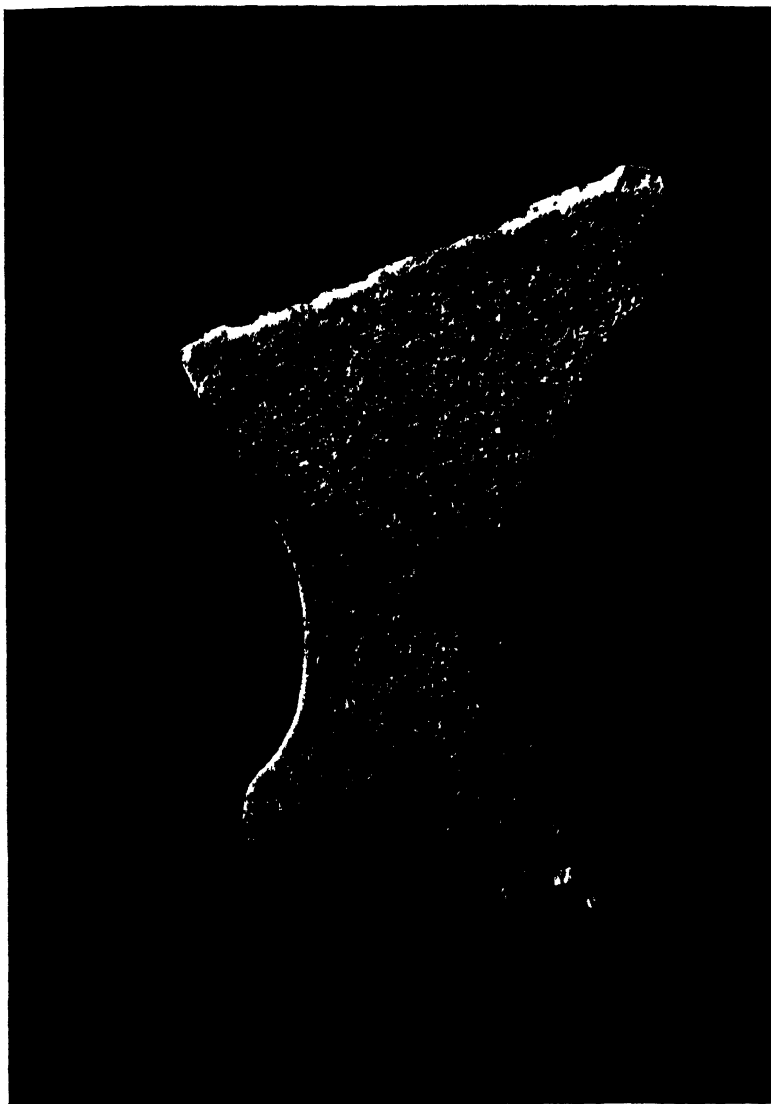
THE FRONTAL SECTION OF THE ILIUM OF TESTDO

The plate shows the cancelli in position, equivalent to the lines of stress shown in Figure 14A. This figure also shows the analogy of the ilium to a hollow column. Note that the ectal wall (region of compressive stress) is more heavily built than the ental wall (region of tensile stress).



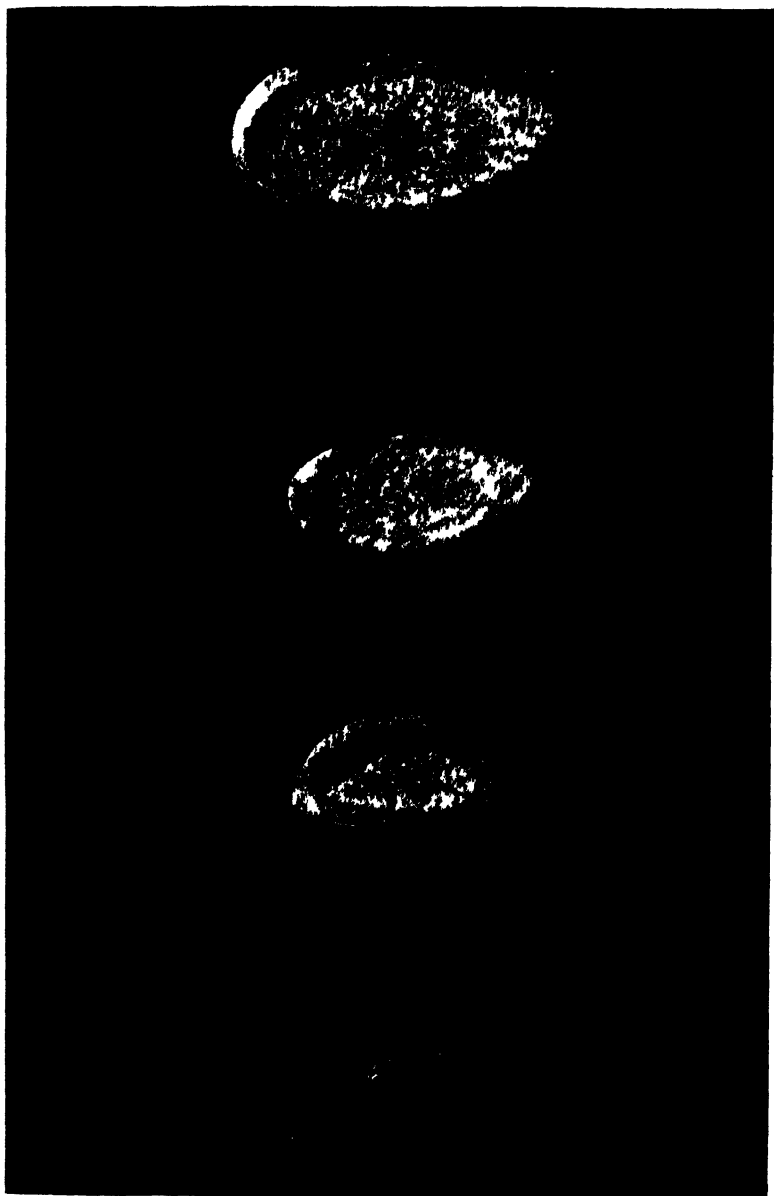
FRONTAL SECTION OF THE ILIUM OF CHELONE MIDAS

Chelone mydas represents the swimming type of turtle. Note that while the os spongiosum is unlike that in *Testudo*, the pattern of the cancelli is much the same. Only the proximal end of this ilium has, as yet, been analyzed.



FRONTAL SECTION OF THE ILIUM OF CHELYS FIMBRIATA

This illustrates a third type of os spongiosum. No analysis of this ilium has been attempted. In the lower right hand portion of the plate is an indication of the way in which the cancelli of the ilium have become contiguous with those of the ischium. The small splinter of bone securely hold the various elements of the girdle in rigid position, and transmit stresses from the ilium to the ischium.



CROSS-SECTION OF THE ILIUM OF TESTUDO

The plate illustrates the hollow column, the center of gravity, the variation in the thickness of the outer wall and the nature of the os spongiosum. The sections are equivalent to sections 2, 4, 6, 8 in Figure 13.

STUDIES IN CHELONIAN OSTEOLOGY

PART II

By HERBERT RUCKES

THE MORPHOLOGICAL RELATIONSHIPS BETWEEN THE GIRDLES, RIBS AND CARAPACE*

CONTENTS

	Page
Introduction	81
Materials and methods.....	83
Historical résumé	84
Outline of the problem.....	85
Factors determining the enclosure of the girdles.....	89
The depression of the body.....	89
The association of the ribs with the carapacial dermis.....	96
The horizontal displacement of the ribs.....	100
The phenomena associated with the depression of the body.....	109
The changes in the coelom shape.....	109
Changes in shape of the elements of the pectoral girdle.....	112
Fossil evidence bearing on the problem.....	115
Summary and conclusions.....	117
Bibliography	118

INTRODUCTION

One of the most characteristic anatomical features presented by the Chelonia represents a greatly distorted morphological relationship between the pectoral and pelvic girdles, the ribs and the carapace. In short, this distortion is carried to the extent of having the girdles placed in planes that are mesad of the ribs rather than lateral of them. This condition has existed in the Chelonia from very early geological times and is not equalled in any other order of craniate animals, and but poorly paralleled. In any generalized vertebrate the pectoral girdle overlies the shafts of the ribs and is attached to them by means of intervening muscle masses. The Chelonia have become so specialized that the shafts of the ribs have been displaced to overlie the elements of the girdle. The costal elements that normally would be found mesad of the girdle have either atrophied or disappeared and the adjacent musculature has

* The publication of this paper has been made possible through a grant from the income of the Esther Herrman Fund.

become piled up in pyramidal fashion upon the cylindrical scapula. While the pelvic girdle still articulates in the normal way with the sacral vertebrae, the pre-sacral ribs have been so displaced as to form a cover over the ilio-femoral region. With the formation of an extensive dermal carapace (which becomes morphologically part of the costal skeleton and has the potentiality of forming a heavy bony armature) the superficial musculature of the body becomes reduced and the girdles become enclosed dorsally by a prominent shield. On the ventral side of the body the development of a plastron accentuates the enclosing of the girdles and completes the boxlike shell.

Several factors of growth and differentiation appear to be involved in the complicated procedure which results in the aforementioned enclosure of the girdles. These factors make their effect felt more or less simultaneously, so that it is difficult to determine what their causal relationships might be. That the displacement of the ribs plays a certain part in the process can be seen by examining the internal surface of a turtle shell. The pelvic region as well as the pygal is often crossed by the last few pre-sacral ribs. A second factor, the coalescence of the dermal carapace with the ribs is so characteristic of the order that mere mention of it here is all that is necessary. A third factor, the reduction of the costal elements adjacent to the pectoral girdle, can be seen by a second examination of the internal surface of the carapace. To these factors must be added another, a growth factor that appears to control the body form of the animal and which results in the formation of a depressed body in the representatives of this order. It appears that this depression is a result of the unequal growth of the body in two of its main axes, the dorso-ventral and right-left. Through the former of these the body grows more slowly than through the latter.

In the course of studies in Chelonian anatomy numerous problems have presented themselves. To the writer the attempt to solve the question relating to the mechanics of the origin and development of the anomalous relationship between the ribs, the carapace and the girdles has been a task of great interest, for, if successfully solved, the results promised to contribute much to a better understanding of chelonian morphology. For this reason, attention was focused upon the problem of determining by what means the pectoral and pelvic girdles become encased within the shell of the animal and of explaining satisfactorily the causal relationship between the various factors of growth and differentiation that contribute to this phenomenon.

MATERIALS AND METHODS

It has been obligatory, of course, to study fossil turtles in order to understand the earlier stages of evolutionary history and specialization. But for the most part recent forms have been used, since the problem deals essentially with a developmental process. Moreover, few fossils are sufficiently different from our recent species to give any hint as to the possible origin of the anomalous organization. The material was studied in different ways. Dried skeletons and dissections of young and adults were satisfactory, but the best interpretative material was procured from stained and cleared specimens made according to the Schultze and Spalteholz processes. In these preparations the body is not only transparent but the tissue remains tough enough to permit dissection in localized areas without injury to adjacent regions. For clearing, medium and late stages of embryos and younger stages of adults were used; toluidin blue was employed to stain the cartilage elements and sodium alizarin sulphonate to stain bone.

In order to check up on the developmental processes studied in whole animals, serial sections of embryos of various ages were used and from some of these reconstructions were made.

For the studies of adult skeletons the following forms were used: Fam. Dermochelidae (*Dermochelys*), Fam. Chelydridae (*Chelydra*, *Macrochelys*), Fam. Kinosternidae (*Kinosternon*, *Aromochelys*). Fam. Testudinidae (*Malacoclemmys*, *Deirochelys*, *Chrysemys* and other Emydid forms, *Terrapene*, *Testudo* and *Kinixys*), Fam. Cheloniidae (*Chelone*, *Caretta*, *Eretmochelys*), Fam. Trionychidae (*Trionyx*, *Amyda*), Fam. Pelomedusidae (*Pelusios*, *Podocnemis*), Fam. Chelydidae (*Chelys*, *Chelodina*). *Dermochelys* represents the Atheca; the Chelydridae, Kinosternidae, Testudinidae, Cheloniidae are examples of cryptodirous Thecophora; the Pelomedusidae and Chelydidae belong to the pleurodirous Thecophora. The Trionychidae represent the Trionychoidea.

For dissection there were used: *Chelone*, *Chelydra*, *Pseudemys*, *Terrapene* and *Amyda*.

Cleared preparations of embryos and young adults were made of: *Caretta*, *Pseudemys*, *Chelydra*, *Kinosternon*, *Gopherus*, *Amyda*, *Pelusios* and *Podocnemis*.

In serial sections, embryos of *Caretta*, *Chelydra*, *Gopherus*, *Pseudemys* and *Kinosternon* were cut in varying thicknesses from 15 to 25 micra.

I am indebted to The American Museum of Natural History for the opportunity to study its collection of the Chelonia, which is in charge

of Dr. G. K. Noble. I wish to express my thanks to him for the permission granted.

For the study of the fossil *Chelonia* the collections at the American Museum of Natural History were available, but the earlier forms in European collections could be studied only from the papers dealing with the individual species.

HISTORICAL RÉSUMÉ

Very little attention has been paid to the analysis of the present problem in spite of the fact that in the adult morphology the relationship between the girdles and the ribs is one of the most striking anomalies in vertebrate anatomy.

Rathke ('48) in describing the later stages of growth and differentiation in turtles did not explain in detail his analysis of the incorporation of the girdle within the shell of the animal, but confined his remarks to the statement that the girdles do not lie in the coelom proper, which at first hand appears to be the case. That impression is due to the fact that in its growth the shell carries the superficial layers of the body tissues anteriorly and posteriorly. These, in turn, attaching themselves to the bony envelopes of the girdles, subsequently pull the girdles deeply into the body wall to give the appearance of actual penetration of the coelom.

In this interpretation, Rathke is partly correct. I feel certain, as will be shown later, that the girdles remain in place and are not pulled in but instead are overgrown by the surrounding parts of the body.

Vialleton ('24), while accepting Rathke's view, appears to believe that the girdles really lie in the body cavity but gives no explanation of how they got there.

Watson ('14), on the other hand, seems to attach no value to either of the above ideas and is inclined to interpret the situation by having the girdles migrate under the shell of the animal. In this way the girdles get under the ribs and move past the mesal surfaces of them, the pectoral girdle migrating posteriorly, the pelvic girdle moving anteriorly. Watson suggests that in order to accomplish this feat the composite two halves of the girdles have to become very narrow; he overlooks the fact that, when the two halves are taken side by side, the chelonian girdles are usually much wider than those of any other reptile except probably some of the Dinosaurs. Watson offers no explanation concerning the peculiar position of the trunk ribs, which in *Chelonia* are displaced from

the normal position that they occupy in other Reptilia. The hypertrophied nuchal and pygal regions Watson interprets as areas of secondary growth over the respective ends of the body.

I believe this interpretation is wholly incorrect and that the girdles do not migrate at all. It is certain that Watson's idea on migration of these parts would explain the occurrence of the very short trunk region characteristic of the Chelonia. Yet, as is to be shown, the pectoral girdle lies opposite a definite vertebra from the time that the girdle tissue is first distinguishable to the time when it is completely ossified. Moreover, other vertebrates may possess short trunk regions without having the pectoral and pelvic girdles displaced backwards or forwards.

OUTLINE OF THE PROBLEM

• In order to facilitate the elaboration of the points that will be discussed in the latter part of this paper, a general summary of the facts discovered is at first offered.

It appears that certain factors of growth and differentiation are involved in the encasement of the girdles by the shell. These are presented in, what to the author, is their sequence of causal relationships, i. e. the sequence in which they interact. These factors are as follows:

- 1) The formation of the carapace and plastron from the dermis, the radial growth of these parts determining the growth and displacement of associated parts of the skeleton.
- 2) The unequal growth of the body axes, the lateral axis elongating more rapidly than the dorso-ventral, thereby producing a flattening of the body.
- 3) The dorsal "displacement" of the ten pre-sacral costæ (which in turn are regulated in their direction of growth by the radial growth of the carapace; c. f. 1 above).
- 4) The horizontal displacement of the ribs also determined by the radial growth of the carapacial dermis.
- 5) The change in shape and position of the coelomic cavities determined by the unequal growth of the body axes.
- 6) The change in position and size of the cartilage elements of the pectoral girdle, resulting from the depression of the body.

Before going into the details of evidence, it seems desirable to take the above résumé and, elaborating upon it, to form a fuller outline of the inferences that can be drawn from them.

- 1) The formation of the carapace and plastron.
 - a) Chelonia of all modern orders, no matter how arched or how flat the adults may be, start their early embryonic life with body proportions not unlike those of any generalized vertebrate, i. e. the dorso-ventral axis is greater than the lateral axis (Fig. 2).
 - b) The carapacial dermis appears in the earlier stages as a very thick layer of tissue, handlike in form, lying in the mid-dorsal portion of the body, extending between the pectoral to the pelvic girdles (Fig. 1).
 - c) Growth takes place in two directions: 1) latero-ventral, causing the dermal layer to extend over the lateral walls of the body (incidentally producing an involution of the underlying wall of the body); 2) antero-posterior, causing the carapace to extend over the two girdles. Together, these two methods of growth result in the encasement of the girdles from the dorsal side of the body.
 - d) Coincident with the origin of the carapace the plastron appears as a thinner layer of the dermis, in the earlier stages more or less following the contour of the organs lying just dorsal to it, i. e. the plastron at first is not the platelike structure found in the adult (Figs. 1, 4).
 - e) The plastron flattens as the carapace grows over the sides of the body and in expanding extends anteriorly and posteriorly beyond the region of the girdles, thus enclosing them from the ventral side (Figs. 3-6).
- 2) The unequal growth of the body axes.
 - a) While the body proportions of a modern chelonian are at first those of a more generalized type, measurements indicate that the lateral growth of the body is more rapid than the dorso-ventral growth of it.
 - b) This unequal mode of development is restricted to the region of the trunk, so that the apparent depression of the body is particularly pronounced in this part of the animal.
 - c) The pectoral and pelvic girdles remaining in situ, the entire somatic portion of the body and adjacent coelom grow laterally beyond the limits of them, emphasizing the enclosing of them within the wall of the body.
- 3) a) The ribs, starting as the short transverse masses of cartilage, are prevented from following their normal course of growth

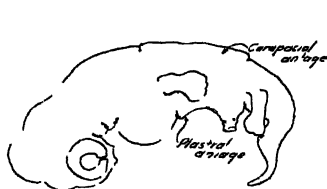


Fig 1

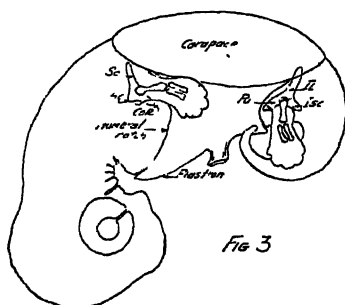


Fig 3

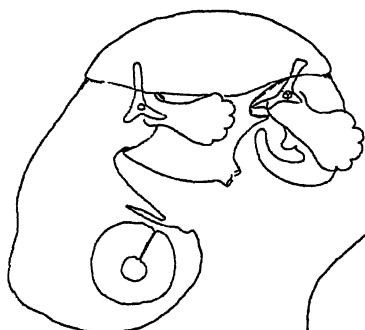


Fig 4

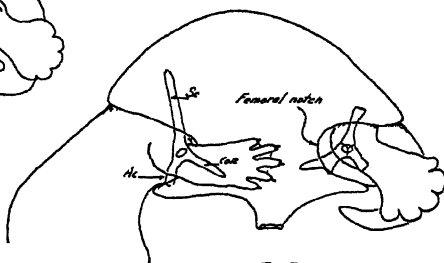


Fig 5

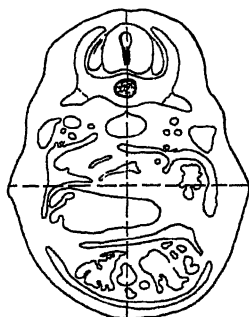


Fig 2

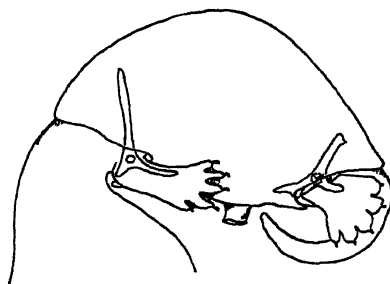


Fig 6

• FIG. 1.—6 mm. *Chelydra* embryo showing the anlage of the carapacial and plastral shells. Late limb-bud stage.

FIG. 2.—Cross-section of *Chelydra* slightly older than that shown in Fig. 1. Diagrammatic to show the body proportions similar to those of a generalized vertebrate. Lung-bud stage.

FIG. 3.—9-10 mm. *Chelydra* embryo with humeral and femoral notches wide open; girdles just beginning to be enclosed by the shells.

FIG. 4.—12.0 mm. *Chelydra* embryo with humeral and femoral notches closing about the limb bases; shell engulfing girdles. Plastron still with irregular contour.

FIG. 5.—15.0-18.0 mm. *Chelydra* embryo with humeral and femoral notches narrowed down and the girdles well covered by the carapace. Plastron in the process of flattening.

FIG. 6.—20.0-25.0 mm. *Chelydra* embryo with humeral and femoral notches closed and the girdles enclosed by the shells. Plastron quite flat.

Abbreviations: Ac.—acromion process, Cor.—coracoid, Il.—Ilium, Isc.—Ischium, Pu.—pubis, Sc.—scapula.

because they become morphologically associated with the carapacial dermis. They are consequently "directed" into a line of growth by the lateral expansion of the carapace and body. This causes the morphological axis of each costal shaft to remain very high on the lateral side of the body, giving each rib the appearance of having been dorsally displaced. So high are the sternal ends of the ribs that they at first extend dorsal to the superior edges of the scapula and ilium.

- b) The lateral growth of the body is so rapid that the ventrally growing ribs are unable in their normal position to develop a "deep-chested" animal.
- 4) The horizontal displacement of the ribs.
 - a) During the earlier stages of the embryo the shafts of the ribs almost invariably meet the vertebral column at right angles.
 - b) Radial or horizontal displacement is first evident as a backward shifting of the axes of the presacral ribs. Two changes are thus brought about: (1) the articulation between rib and centrum is shifted and (2) the direction of the growth of the shaft is altered.
 - c) The result of these changes causes the pelvis and the femoral region to be overgrown by the last few trunk ribs, thus altering the normal relations between these parts of the skeletal system.
 - d) In some species a radial displacement occurs in the region of the shoulder girdle. This may be in two forms: 1) an almost universal type, in which the first trunk rib bends posteriorly to form a brace on the longer second rib and 2) a not very common type, in which the second rib is pulled well forward so that its shaft cuts across the whole shoulder and basal neck region. The latter has been termed the *Trionychid* type from its prevalence in that group of turtles.
- 5) Change in the shape of the coelom.
 - a) Due to the persistence of the generalized pattern of the body plan in the earlier stages of development, the abdominal or peritoneal cavity lies in its normal position, mesad of the pectoral and pelvic girdles and, anteriorly, entirely dorsal of the pericardial chamber.

- b) As the body expands laterally and the apparent depression ensues, the coelom is pushed posteriorly and begins a lateral overgrowth of the post-scapular elements of the pectoral girdle.
 - c) The lateral expansion of the coelom and its overgrowth of the coracoid give the erroneous impression that the girdles have been pushed internally into the body. There always persists a much reduced remnant of the body wall between the girdle elements and the body cavity proper.
 - d) In the pelvic region the expansion of the coelom occurs only anterior to the girdle and does not completely envelop the pelvis.
- 6) Change of the shape of the girdle as an aid to its enclosure.
- a) The pectoral girdle first appears well up on the lateral side of the anterior trunk region.
 - b) The girdle does not move either forward or backward, but the fact that the body grows more rapidly in a lateral direction than a dorso-ventral one, causes an outward pull on the girdle. As a result the shoulder girdle bends or bows, the bending taking place in the region of the glenoid fossa. In this way the acromion process becomes inbent under the plastron and, as the depression of the body continues, the two halves of the pectoral girdle become further squeezed between the plastron and carapace.

FACTORS DETERMINING THE ENCLOSURE OF THE GIRDLES

THE DEPRESSION OF THE BODY

In studying the developmental anatomy of the Chelonia, one is immediately impressed with the fact that, no matter how arched or flat the adult animal may be, each species begins its early embryonic development with body proportions not unlike those of a generalized vertebrate (Fig. 2). That is to say, the body is slightly compressed from right to left and is normally quite deep through the dorso-ventral axis. Correspondingly the internal organization of these animals follows a plan laid down for the generalized reptile type. The fact that most adult Chelonia are flattened to some degree is immediately an indication of specialization of the animal as a whole. Depression to any extent could not be accomplished without an extensive rearrangement of the more

rigid skeletal parts as well as of the viscera and softer organs. A parallel to the Chelonia is seen in several lines of specialized fish. The ray as a type of specialized elasmobranch illustrates such a rearrangement of parts when compared with the more generalized shark. In just the same manner the chelonian must adjust its internal organization to fit its external contour. While the organs of the digestive tract, blood vascular system, urinary and genital tracts and the nervous system are able easily to accommodate themselves to the necessary changes, they are not particularly aberrant in animals of unique shape. It is only in the less pliable skeletal system that anomalous changes can be expected to occur. In this system, particularly, the Chelonia have carried specialization a long way, and without a doubt to the greatest extreme of any of the chordates.

The flattening or depression of the body has a direct bearing upon the solution of the problem previously outlined. So important is this phase of the subject that it is the basis of the explanation of all the later changes that occur during the embryonic development and differentiation. It is necessary, therefore, to understand accurately how the depression of the body starts, what procedure it follows, which systems are directly affected and which are concerned only secondarily with the flattening.

To state briefly the entire mechanical analysis of the flattening is obviously impossible, since it is a very involved affair. For simplicity in the discussion it might be well to mention at this time that the main principle upon which depression of a body depends is, that the animal grows unequally in its various axes. In the case of the Chelonia the animal, although starting off in life with normal body proportions, shows the observer a dorso-ventral axis and a right left axis in which the former is longer than the latter. If growth proceeds equally in each of these two axes or directions or parallel to the axes, then the primitive body shape is retained. But, should one or the other of these axes be a line of growth of greater magnitude and rapidity, then the body shape transforms from the original pattern and a new body contour results. Just so in the Chelonia, for here the growth in the lateral axis is far more rapid than that in the dorso-ventral.

The inequality in the growth of the body results in an approximation of the plastron to the carapace. In reality the plastron never approaches the carapace so closely that their inner faces touch, for there is a continued but slow growth of the body in its dorso-ventral axis. Neverthe-

less the rate of growth of the animal in lateral diameter is a mathematical function of the rate of growth in its vertical direction. As this function varies, the definitive contour of the adult animal will vary and either highly domed forms like *Testudo* or very depressed forms like *Amyda* occur.

The actual procedure that results in the depressing of the body can be followed by studying the growth and differentiation of the carapacial and plastral dermal layers. In the early embryonic stages, when the anlage of the carapace and plastron first make their appearance, these layers are widely separated from one another (Figs. 1, 2, 3). As the animal grows, the carapacial layer seems to pull away from its original position and tends to take the underlying parts of the body with it. It seems to pull away rapidly in a lateral direction, so that the animal at successive stages shows the dermal layer piling up at the lateral edges of the carapacial anlage, while the dorsal and median portions become somewhat attenuated. The plastron follows the method of the carapace but is not so readily observed because of its relative thinness. In this way the lateral edges of the anlage of the shell, if pulled far enough laterally, begin to approach each other. In doing so they have the appearance of squeezing the intervening parts of the body between themselves, and of giving to those parts of the body a more or less abnormal position and contour.

With the exception of the ribs, which are derived from the endoskeleton, the various parts of the turtle shell are of dermal origin. The part of the dermis giving rise to the shell is of very specialized mesenchymatous nature. The cells are at first of the ordinary embryonic mesenchyme type, more or less stellate with long fibrous strands extending in all directions. As the tissue condenses, the stellate cells become fusiform, first stout and short, then very long and thin and take on the ability of growing more rapidly than the cells of the surrounding tissues. Moreover, the cells compact a great deal and form a mass that, by virtue of the rate of the aggregate growth of the individual cells, will be able to advance rapidly in whatever direction is determined by the position of the largest number of cells. These being at the lateral edges, the most rapid growth is in a lateral direction.

The differentiated dermal layer does not make its appearance until the embryo is well along in the limb bud stage. In *Chelydra* this occurs when an embryo is about 8.5 to 9.0 mm. long. At this time, that portion of the dermis destined to produce the shell appears as a ring or band about the middle of the body, being more easily recognized as a thick

ridge along the mid-dorsal part of the animal. The thickened ridge extends between the pectoral and pelvic regions but really does not overlap them. Laterally, the ridge thins out over the sides of the body to form the anlage of what is later to be the bridge of the shell. This thinner layer in turn continues over the venter of the body and there forms the rudiment of the plastron. While these parts form one continuous girdle around the middle of the body, growth in the different regions varies because most of the cells accumulate at the lateral edges of the dorsal and ventral ridges. This portion then begins a rapid movement over the lateral portion of the body, while the anlage of the bridge, with its relatively thin layer of cells, grows more slowly. Very soon the lateral edges of the carapacial anlage extend beyond the dorsal edge of the bridge region, frequently causing an involution of that part of the body. In more or less similar fashion the plastral anlage grows laterally but at a slower rate than the carapacial layers. The result of this type of growth is that the anlagen of the bridges are "carried" to positions more lateral than those they originally occupied and so take with them the underlying body contents and coelom. It appears that the hyoplastral and hypoplastral regions grow at a rate that keeps pace with the growth of the dorsal shell and, since these regions of the plastron are in contact with the bridge regions, they help to "push" the bridge laterally; hence in the usually flat turtle long narrow hyoplastral and hypoplastral elements are to be found while in the much arched types these plates are short and stout. The epi-, ento-, and xiphi-plastral regions appear to have a growth rate of their own, and this is varied in the different species.

As stated previously, the carapacial dermis lies as a thick ridge of tissue along the mid-dorsal line of the body. In cross-section it is easily recognizable, its thickened lateral edges protruding beyond the lateral limits of the body and microscopically distinguishable from the surrounding tissues by its mesenchymal appearance. This anlage grows in two directions. One of these is in a latero-ventral course and will be so termed in the remainder of this paper; the other is in an antero-posterior direction. In forms like *Chelydra*, *Chrysemys* and *Kinosternon* the incipient stages of growth in the latero-ventral direction are apparent at 8.5 mm. and by the time the 10.0 mm. stage is reached the outline of the layer is such as to be recognizably that of a carapace. In that portion of the body anterior and posterior to the bridge anlagen the rate of growth of the carapacial dermis may be determined by the rapidity of the involution of the underlying body wall (Fig. 7). As the dermis

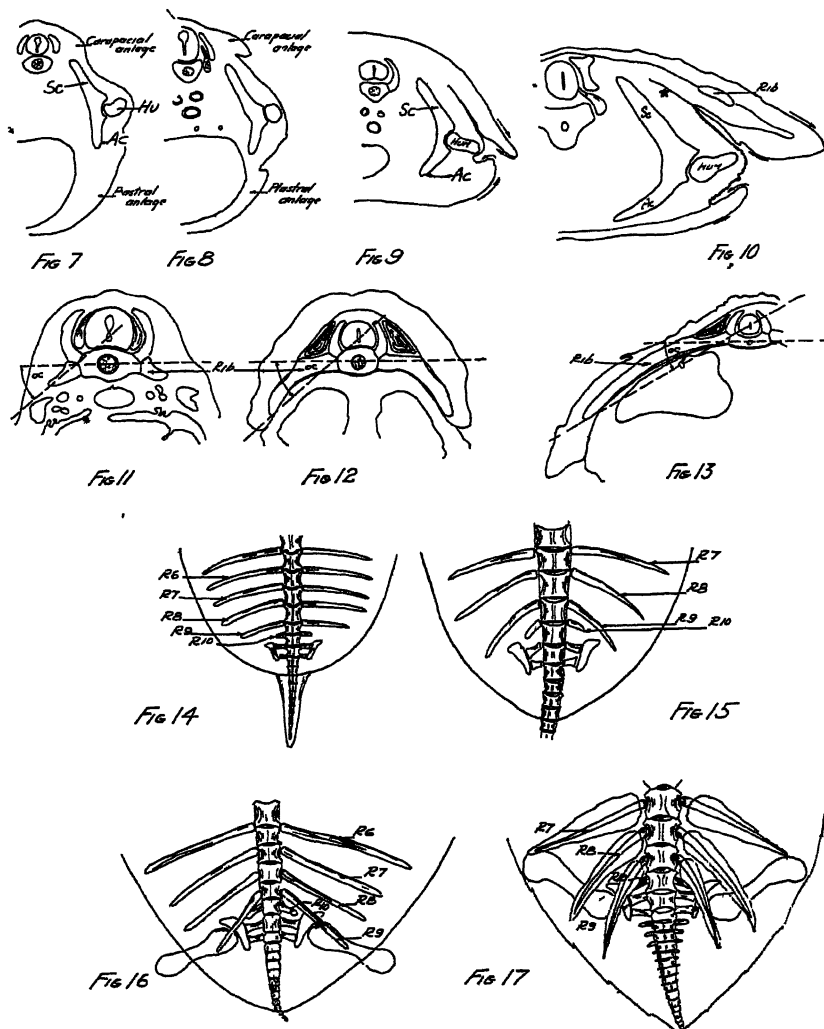


FIG. 7.—Cross-section diagram to show the dorsal and lateral position of the pectoral girdle. About 8.0 mm. *Chelydra* embryo. Similar condition is found in *Caretta*, *Gopherus* and *Amyda*.

FIG. 8.—Carapace and plastron exhibiting lateral expansion and involution of the dermis around the limb base. *Chelydra* embryo about 10.0 mm.

FIG. 9.—Depression partly completed. Girdle bending at the glenoid region and the dermis involuted about the limb base. *Chelydra* 12.0-13.0 mm. embryo, which is approximately equivalent to a 15.0 mm. *Caretta* embryo.

FIG. 10.—Depression of the body completed. Involution of the dermal wall still evident, though at the upper recess (*) the outer and inner wall have coalesced and buried the underlying musculature. Girdle well bent and approaching the adult pattern. *Chelydra* 18.0 mm.

FIGS. 11-13.—Illustrating gradual "raising" of the ribs from their normal position. The angle α becomes more acute as the development advances. Diagrams are based upon a series of *Chelydra*, *Caretta*, *Gopherus* and *Pseudemys* embryos.

FIG. 14-17.—Series illustrating the radial or horizontal displacement of the presacral ribs. Fig. 14 represents a 8.5 mm. *Chelydra*; Fig. 15 a 9.5-10.0 mm. *Chelydra*; Fig. 16 a 15.0 mm. *Chelydra*; Fig. 17 a 30.0 mm. *Caretta*. All dorsal views, showing dermal plates forming about each costal cartilage.

Abbreviations: Ac.—Acromion process; Hu—humerus; R6-R10—Sixth to tenth trunk ribs; Sc.—scapula. α —angle formed between the transverse diameter of the epimerous part of the body and the axis of the incidence of the rib and vertebra.

grows over the sides of the body, it does so in a "flowing" fashion, reminding the observer of a very viscid substance being poured over the animal and gradually spreading out over the body. The superficial layer of the dermis advances more rapidly than the deeper layer and there appears, in consequence, to be an infolding of the body wall. In reality it is only the dermis that is folding in on itself. Nevertheless, in this way the superficial musculature of the limbs and the body (wherever any such body muscles might remain) are buried beneath the thick dermal coat.

Growth in a second direction is manifest in the progressive expansion of the dermis in an antero-posterior axis. The growth in the anterior direction causes this layer to overlap the superior part of the pectoral girdle. Both Rathke ('48) and Watson ('14) recognized this manner of growth. The former studied the problem from the point of view of the activities of the dermis alone and did not seek any correlation between the growth of the dermis and the movements of the ribs, while the latter believed that the expansion of the carapacial shell in an antero-posterior direction was merely a secondary adaptive one. To be sure, the degree of growth of the dermis in both the nuchal and pygal regions of the body is very variable, some species, mostly Emydids, have fairly short nuchal shields while the Pleurodira have large ones. In like manner, the pygal coverings may be expansive (*Kinixys*) or not (*Chelydra*). The present writer sees fit to adopt the following view. The dermis and its growth do not alone tell the complete story, for associated with the dermis are the ribs. These, being pliable structures during their developmental stages, may be distorted at the instigation of the dermis, so that wherever the latter layer grows, thither follow the ribs. In many instances, I think, there is a secondary adaptive value to the growth of the carapacial dermis, especially in its great crested form seen around the pygal region in *Kinixys* or in the "collars" around the nuchal edge of some of the *Testudo*, but the adaptive value is not the primary one.

In the above description, the methods of growth of the heavy carapacial dermis have been termed latero-ventral and antero-posterior; these terms have been suggested because they permit the simplest description of the analysis of the carapace or at least its anlage. It must not be overlooked, however, that these two lines of growth are not independent of each other and that there is no sharp line of distinction between the limits of the two directions. On the contrary, the growth of the dermis is a composite movement of the layer in all directions or in directions

representing two or more axes. In this sense the growth gives the appearance of a radial expansion of the layer. "Radial" infers growth in all directions, starting from a common center, that center being the ridge of carapacial dermis on the dorsal mid-line of the body.

More or less coincident with the changes that occur in the carapacial dermis, the anlage of the plastron goes through a metamorphosis. By means of the bridge region the plastron is in contact with the carapace; but the ventral dermal layer is much thinner than the dorsal one and so more exactly follows the contour of the underlying organs. This condition is most easily observed in the region of the embryonic heart, which, as in all vertebrates, is very large in the early developmental stages. Two directions of growth are apparent again in the plastron; these are similar to those found in the carapace. I do not believe that the plastral dermis has the same initiative power as the carapacial, but that it more or less follows the lead set up by the lateral movement of the bridge portion of the shell, since that is being laterally displaced by the rapidly expanding carapace. The growth of the plastral wall is sufficient, however, to permit it to flatten out and eventually become plate-like, thereby losing its irregular or bumpy contour. Incidentally during the growth of the plastron, an involution of the body wall similar to that accompanying the growth of the carapace occurs with the result that the ventral body musculature is overgrown by the plastral dermis much as the dorsal musculature is covered by the carapacial. Growth in an antero-posterior direction permits the plastron to work its way over the ventral surfaces of the pectoral and pelvic girdles (Figs. 3-6).

More interesting than a mere study of the lateral and radial growth of the dermal layers is the actual observance of the progressive stages of the depression of the body as a whole. This can be most readily studied from a lateral aspect. The anlage of the bridge region is unable to follow the extensive antero-posterior growth of the carapacial and plastral layers, because the humerus of the front limb and the femur in the hind stick out laterally from the sides of the body. In the course of the growth of the shell, therefore, the anterior and posterior edges of the bridge fall far behind the same limits of the other parts, leaving what is termed a humeral and a femoral notch in the lateral wall of the shell. The latero-anterior edge of the carapace extends quite obliquely dorsad from this notch as the plastron extends in a like manner ventrally. An analogous condition is found in the femoral notch. In the early developmental stages the outline formed by the edges of the carapace, notch and plastron at both the anterior and posterior ends of the

shell reminds one of a pair of widely distended jaws, which, when viewed from the proper lateral aspect, seem to be about to close upon the girdles that lie mesad and directly adjacent to the notches. As the embryo progresses in its development, the edges of the carapace, notches and plastron gradually approach one another until they are folded to such a degree that the plastral and carapacial edges almost touch. This procedure heightens the impression that the edges of the notches act as a pair of jaws closing on some contained object. The rate of the closing varies in the different species but is sufficiently slow to enable one to detect it in the growth stages of the embryo from 10.0 to 20.0 mm.

It is only after these notches become completely closed that it can be said that the girdles are hidden under the shell, for until the closing is accomplished, the girdles remain visible from the lateral aspect of the animal.

While all the changes that have been just described are taking place, the dermal layer is in a mesenchymal state, at first loosely reticulate and subsequently denser and more fibrous. The condensation of the cells to form bony elements does not occur until a period well after the shell has been completely outlined. Since the discussion of the origin and development of the dermal bones is not in the province of this paper, this phase of the discussion may be terminated here with the brief statement that the enclosure of the girdles is accomplished long before the carapacial and plastral bones make their appearance.

THE ASSOCIATION OF THE RIBS WITH THE CARAPACIAL DERMIS

The costæ, strictly of endoskeletal origin, are from a very early stage of embryonic development in close association with the carapacial dermis. The innermost layer of the skin is in juxtaposition to the superficial wall of the ribs, so close, in fact, that the normal intercostal and cutaneous musculature fails to develop. With the condensation of the dermal tissue a still more intimate contact with the ribs is brought about and thus the latter organs enter into an inseparable physiological association with the skin (Fig. 8). It is obvious, then, if the ribs are in such close contact with the potential carapace, that whatever course of growth the dermis takes, the ribs will be forced to follow to a greater or lesser degree. The phenomenon of the movement of the costæ is readily observed and in this paper is termed *displacement*. This term is employed to indicate that, once the rib has been moved from its primitive or embryonic position, it does not return to that place. The

term also carries the implication that the ribs are shifted out of their normal position and assume new positions, which are determined by the rate and degree of dermal expansion. Correspondingly, the rate and the direction of the growth of the ribs vary.

Two such displacements have been recognized in the development of the chelonian ribs. One of these is termed *true displacement*, by which is meant that the ribs are actually shifted out of position, with the surface of articulation between the rib and the centrum being used as the fulcrum for the movement. The second type is more difficult to describe because there is no true shifting involved but merely a change in the direction of growth of the shaft affected. This type has been termed *pseudodisplacement* and does not include the transposition of the ribs and facets. Moreover, the term pseudodisplacement implies that there is an apparent shift but not a real one. The apparent movement is credited to the fact that the anlage of the ribs prevents them from following their normal path of growth and that they are retained in a position much more dorsal on the sides of the body than is common for generalized vertebrates. This is possible since the cartilage rudiments of the costæ form the intimate contact with the dermal layer of the carapace, as was previously mentioned, and are thus forced to grow laterally (instead of ventrally) as rapidly as the dermal layer advances in that direction.

It is this second mode of determinative growth that is misleading in the interpretation of the relationship of ribs and girdles. Until early enough stages of growth were studied, it was a puzzle to understand how the ribs could assume a position so high on the lateral sides of the body as is characteristic of the Chelonia. In most reptiles the ribs curve around the body, extending from the backbone to the ventral sternum. In such forms the shafts of the ribs lie in more or less vertical planes and meet the backbone in pronounced arcs. But in the Chelonia the ribs never meet in the mid-ventral line and there is no true sternum. Instead, the costæ stretch far to the sides of the body in slightly curved arcs, so that their distal or "sternal" ends, after the completed growth, are finally able to reach well beyond the lateral limits of the girdles. In this way, while the curvature of the rib is still in a vertical plane, the shafts have straightened out to such an extent as to give the impression that each costa has been dislocated dorsally to accept a position higher up on the wall of the body. Although the direction of the growth of the shaft has been changed, the articulation between the

costal element and the vertebral column has not been altered, for the head of the rib is not attached to any more dorsal part of the centrum in the adult than it was in the early embryo, when the costal cartilage first became differentiated. The question concerning this false displacement is particularly vital for a correct interpretation of the anomalous relationships existing between the ribs, carapace and girdles, and so it becomes necessary to investigate by what means the more dorsal position of the ribs is attained.

As was intimated above, the ribs from their very earliest stages of differentiation are in close association with the carapacial dermis, and their growth is determined by the rate and direction of the expansion of that layer. In studying the early stages one fact is brought to light; that is, in the beginning the ribs are very short stout lateral projections from the vertebral column, which meet the column almost at right angles, and are never long enough to curve laterally around the body to meet in the mid-ventral line and enclose a thoracic region, as the ribs do in normal tetrapods (Fig. 27). The thick dermal carapace lies directly dorsad of the surface of the ribs, and in growth gradually envelops them with a thin sheath of its own cells. This fact prevents the ribs from working their way around the sides of the body, as happens in other generalized tetrapods, but causes them to be guided into continuing their growth in a transverse or lateral course as the carapace itself expands in that direction. While the incipient rib is quite short, that of the adult is rather long with its arc of curvature depending upon the degree of flattening of the whole body. In no *Chelonia* does the degree of curvature approach that found in animals in which the ribs meet ventrally in a sternum.

In their incipient stage the short stubby ribs do not extend laterally beyond the limits of the girdles. In the course of their growth they are able to extend farther laterad so long as there is nothing in the way to hinder their doing so, and they will continue to grow as far to the sides of the body as the carapace expands in that direction. In the anterior region, however, the scapula of the pectoral girdle lies opposite the first rib and in the posterior part of the trunk the ilium of the pelvis lies close behind the last one. The proximity of these structures affects the final size of these respective ribs. In the case of the anterior one, the whole shaft is shifted posteriorly so that it will be able to grow laterally beyond the scapula, the rib itself being apparently unable to push the scapula aside, but the proximity of the latter organ seems to inhibit the

full growth of the rib and the costa permanently remains quite short. Similarly in the case of the most posterior trunk rib, the proximity of the ilium prevents the complete elongation of the rib's shaft, and we find that like the most anterior rib, the posterior one is short and abortive.

It must be kept in mind that in the *Chelonia* the scapula is of very specialized form and is anatomically unique. Its most typical form is cylindrical with a slightly tapering superior end. Moreover, it is provided with a very large acromion process, which sticks out from the glenoid region much as does a procoracoid element in other tetrapods. The cylindrical form of the scapula appears to be an adaptive feature, which is coupled with the adaptive necessity of having the ribs retained in a high lateral position so they are able to grow toward the sides of the carapace far beyond the lateral limits of the girdles. A broad triangular scapula would most grossly interfere with the desired growth of the ribs that would be found adjacent to it. If these underlying ribs were prevented from growing laterally because a scapula barred the way, then the entire carapacial region laterad of the triangular scapula would be without support and reinforcement and in such a condition would certainly be very weak and probably not substantial enough to withstand the surface pressures that are ordinarily exerted upon it. The narrow, cylindrical scapula more or less solves the problem of how the anterior shoulder region of the carapace might be reinforced by the shafts of the ribs, for in this instance we can see by inspection that only a single rib lies adjacent to the superior part of the scapula, and the reinforcing value of the single rib might easily be transferred to one just posterior to it, so that but little of the shoulder region of the carapace is left unsupported. If, on the other hand, the scapula were to persist in the *Chelonia* in its normal position, i. e. always ectad of the shafts of the ribs, and the body form of the animals maintained its present proportions, then the scapula would have to be carried far to the superior part of the carapace and, thus placed, would be in no position to aid as part of the locomotor apparatus.

From what has just been described, one might be led to the conclusion that the scapula assumed its cylindrical form for the express purpose of falling internally through an intercostal space. This interpretation is incorrect, I believe, in view of the evidence procured from the study of the ontogenetic development of the ribs and the so-called pseudodisplacement of their shafts. A truer explanation, I think, is that the scapula has remained in its original embryonic position while the ribs

have grown above it and to the side. But the ribs would not be capable of growing in this direction were it not for the fact that they join forces with the carapacial dermis and are led in whatever direction the growth of the latter layer takes.

THE HORIZONTAL DISPLACEMENT OF THE RIBS

Although the costal elements have been growing laterally beyond the limits of the girdles, we must not overlook the fact that the carapacial dermis is not limited to a lateral growth alone. In order to produce the desired body proportions the dermal layer expands in an antero-posterior direction as well as laterally, and gives the observer the impression of a slow radial expansion. The growth of the carapace in the antero-posterior direction must next be described and an analysis must be made of whatever effects this type of growth will have on the underlying organs. In the meantime it must not be forgotten that the ribs have been morphologically and physiologically united with the inner wall of the dermis.

It seems that there is no definite formula or law that can be established to designate the rate of growth of the dermis in the antero-posterior direction as compared with its lateral growth. Some *Chelonia* are broad, short-bodied forms in which the lateral growth of the carapace is relatively more rapid than its longitudinal growth, while others are long-bodied forms with rather narrow proportions, in which the reverse ratios of growth must exist. There are still others that are nearly equiradiate and the growth is apparently equal in all directions at once. However, this much must be understood, that the carapacial dermis (as well as the plastral) is at first restricted to the region of the body roughly limited by the pectoral and pelvic girdles, and that the dorsal dermis certainly does not overlap the girdles when the latter structures are first visible. But in the definitive body form all *Chelonia* exhibit a state in which the carapace extends well beyond both girdles. It has been found that the girdles always remain opposite a definite rib and its corresponding vertebra. We must conclude, therefore, that the carapace, and the plastron too, have grown longitudinally to overlap these parts of the skeleton. In the longitudinal growth of this layer it seems that the same procedure outlined for the lateral expansion of the layer is followed. That is, the peripheral limits of the dermis are the regions where the cells are in most active division and where they would tend to accumulate. Too great an accumulation would build up a dermis much

too thick for the convenience of the animal, and the result is that the active cells invade new territory still more peripheral to their original position. Again it seems that the superficial layer of the dermis is able to advance more rapidly than the deeper ones so that as the advancement in the growth occurs, there is an involution of the body wall, which in time covers over all the underlying body musculature, and since the dermis will eventually develop bony plates, the musculature either does not become differentiated or, if it does, it soon atrophies.

Now, if we start off with the premise that the ribs have become morphologically a part of the dermal layer, then it can be expected that growth of that layer in an antero-posterior direction will affect the line of growth of the ribs, so that they will be carried in those two directions at the will of the dermis. The longitudinal growth of the dermis takes place while the ribs are in their cartilage stage and while they are still flexible enough to be moved about. As a result, it is found that the costal cartilages begin to be spread out like the stays of a fan, the shifting of the shafts taking place in a horizontal plane and not in a vertical one. The movement is one of *true displacement* since it has been found that as the displacement proceeds, there is a change in the articulation between rib and centrum. It is by means of this horizontal displacement that the pelvic, and in some cases the pectoral, girdle, becomes covered over by the trunk ribs and thus enclosed from the dorsal side. Coincidentally there is a great change in the arrangement of the musculature in the ilio-lumbar region, for the posterior trunk ribs could not very well be displaced without upsetting the whole muscular pattern of the region.

The beginning of the process of horizontal or true displacement can be found in early embryonic stages. At a period when the carapacial dermis is just barely formed (6.0 to 7.0 mm. embryos of *Chelydra*, *Pseudemys*, *Kinosternon*, *Gopherus*) the ribs appear as stout spurs, all perpendicular to the vertebral column, when the animal is viewed from the dorsal aspect. The ribs are almost all of the same length, their lateral growth having not as yet begun. The ten trunk ribs are all parallel with the two sacrals, which extend laterally to the ilium. Just when the horizontal displacement starts is difficult to say, but it is evident that it cannot occur before the ribs have built up an association with the carapacial dermis, and until they lie above the superior limits of the scapula and ilium. It must be stated here that both the horizontal displacement of the ribs and their growth in a lateral direction go on simultaneously and are not independent of each other.

An internal view of the shell of an adult turtle will show that in the middle trunk region the ribs articulate to the backbone at points between two adjacent centra, the ribs being provided with a capitulum for the attachment. The posterior trunk or presacral ribs, however, are attached to the middle of a single centrum, a condition found in only a few of the very specialized tetrapods. In the chelonian embryo, on the other hand, all the ribs are attached to the backbone at points between two adjacent centra. The obvious conclusion is, then, that between the early embryonic stages and the adult, the ribs of the presacral series have been pulled out of their normal position and have been shifted to a more posterior place. Not only is the change evident in the assumption of a new center of articulation for the capitulum, but it is also evident in the new direction into which the shaft of the rib grows.

In the study of the horizontal displacement of ribs several species of turtles have been used. Principal among these are *Caretta*, *Chelydra*, *Gopherus*, *Amyda*. These represent the swimming, generalized, terrestrial and Trionychid types. In all of them the same process of rib origin, rib growth and differentiation takes place. Unfortunately the embryos of the Pleurodira were not available, but on the evidence obtained from newly hatched young and very young adults it seems that the same process of development takes place in this group as occurs in the Cryptodira and Trionychida.

Chelydra will serve as the best example in the description of rib displacement, for this genus is well at the base of the phylogenetic tree of the order of turtles. As was stated, the ribs are visible when the carapace is but 6.0 mm. long. At this time all the costal elements are parallel to one another. They are very short, certainly not extending beyond the lateral limits of the girdles, and all are placed at practically right angles to the backbone. As each element lengthens, it extends into the thick coat of carapacial dermis and becomes an integral part of the latter structure, thereafter never to be dissociated from it. The dermal cells appear to form a thin envelope about the shaft of each costal element and thus prevent it from following its own line of growth and cause it to be directed in its growth movements so that it must follow the course laid down by the growth of the carapacial layer. By the time the carapacial dermis reaches a length of 8.0 to 10.0 mm. the second presacral rib (the first presacral rib is not affected in any of the changes herein described) has had the axis of its shaft shifted, so that now the rib is no longer parallel to those in front of it and its angle with the backbone

is no longer ninety degrees. It seems that the backward shifting of these ribs goes on at a rate equivalent to the backward growth of the carapacial layer over this area. At this time the second presacral rib does not cut across any part of the pelvis but is merely pointing in the direction of the femur. By the time the carapacial dermis is 12.0 to 15.0 mm. long, the same rib can be seen in a more posteriorly placed position. Its shaft now cuts across the most proximal part of the femur in a line vertically above the head of the thigh bone. While this posterior displacement of the second presacral rib is taking place, the two ribs just anterior to it are likewise being shifted out of their original positions and are assuming new positions in which their shafts are bending posteriorly. The amount and rate of divergence of these three presacral ribs is variable, for they are not all displaced at the same time but follow one another in posterior-anterior sequence, the posterior one being the one most displaced from its lateral position. In this way, then, the posteriormost rib is able to bend farther backward than the ones in front of it.

In their incipient stages of formation the ribs articulate between two adjacent centra. By the time the 12.0 mm. stage is reached, the second presacral element has shifted this center of articulation so that the capitulum is moved backwards upon the centrum of the posterior vertebra. Just how the original articulation is broken down has not been determined. When viewed dorsally, the second presacral rib of a 12.0 mm. embryo meets the backbone at an angle much less than ninety degrees and much nearer forty-five degrees. In time the other two more anterior presacral ribs follow the lead of the second, and eventually come to a state of development where the capitulum of each articulates with the middle of its centrum.

By the time the carapace has grown to be 20.0 mm. long, the horizontal displacement of the presacral ribs is entirely completed. At this stage the elements are arranged in such a way that the first presacral is very short and unaffected by the displacement movements, the second presacral cuts directly across the proximal end of the femur while the third intersects the arc produced by the backward and forward movement of the distal end of the femur. Altogether these ribs form a radiating, fanlike covering over the ilio-femoral region and produce a dorsal box-like enclosure for the pelvis. Meanwhile the pelvis has remained in its original position, being held in place by its attachment to the sacral ribs. All theories propounding the encasement of the girdle (pelvis) by virtue

of its inward or cranial migration under the ribs certainly seem false in view of the fact that the actual displacement of the ribs can be so readily followed, step by step.

It is only reasonable to question the purpose of the displacement of the ribs in this region. The dermal carapace, whether it forms bony costal plates or not, is in need of some mechanical reinforcement much as the web of a fan needs wooden or metal stays to keep it expanded and to prevent it from collapsing. In the case of those turtles that form no heavy dermal plates the necessity of some reinforcing rods in the soft dermis is obvious, otherwise the large area of the ilio-pygial region which is covered by this dermis would of its own weight tend to collapse. When it is remembered that there are a large number of external stresses applied to this region of the body, the foresight in placing stays within the collapsible layer is astounding. Even though dermal plates may be developed and may perfectly well fit into one another to form a dome over a part of the body regardless of the presence of supports from beneath, these plates become all the more resistant to external stresses if they can be supported upon the axial skeleton by means of lateral outgrowths (the ribs). The dermal carapace extends so far behind the last trunk ribs and the pelvis that it would have to exist in a weakened and unsupported condition if the last few ribs were not displaced in such a fashion as to give the required strength.

The very last trunk rib—the one heretofore called the first presacral—does not go through any radical movement while its more anterior fellows are being displaced. Two reasons can be assigned for this peculiarity. In the first place, it does not grow in length as do the others. Its abortive size may be accounted for by the fact that the proximity of the ilium as another part of the skeleton exerts an inhibiting influence upon it and prevents its normal extension. As a result of its persistently small size only a very limited part of its distal extremity can enter into the carapacial dermis; not enough of the shaft having entered into contact with the dermis, there may not be enough leverage exerted upon it and the pull of the backward-growing dermis is not sufficient to cause a corresponding movement of the rib. In the second place, if by chance this rib should lengthen and be carried backward like its more anterior fellows, in passing the region of the ilium it would meet obstruction in the form of the ilium itself, as this part of the chelonian skeleton lies within a few millimeters of the rib and frequently has its superior edge expanded to such an extent that the last rib and the ilium almost touch each other.

The radial displacement of the ribs of the anterior trunk region is a more complicated process and not so readily explained as the displacement of the ribs of the ilio-femoral region. Displacement in the pectoral region seems to be of two types. Almost always in the Chelonia the first trunk rib is displaced posteriorly; in a few cases (Trionychids) while the first rib is moved backward, the shaft of the second rib is moved well forward in a horizontal arc.

The universality of the posterior displacement of the first rib may possibly be explained as follows. Its proximity to the scapula may prevent it from growing as long as the rest of the ribs, much as the proximity of the last rib to the ilium prevented that one from elongating. The necessity of producing a support upon the second trunk rib is evident from the fact that that rib is far removed from the nuchal edge of the carapace; that such a support is actually produced by the first rib when it is posteriorly moved out of its original position, is seen by the way the first rib abuts onto the shaft of the second.

While there is a rather constant shifting of the first rib in all the Chelonia, the degree of the displacement varies not only with the different species but actually within a given species. In a series running from *Dermochelys* through *Caretta*, *Chelydra*, the land forms, to the specialized Trionychids, the following progressive stages in displacement may be noted. In *Dermochelys* the first rib is fairly long, almost parallel to the second and not displaced posteriorly. Sometimes it is carried anteriorly. Since there is no heavy bony dermal shell to be held in place, the naked ribs need not be distorted at all to give the desired support to the leathery carapace. In all the other species of the turtles that possess bony shells there is a marked displacement although in *Caretta* this is not so pronounced as in *Chelydra*. In the former the first rib tends to vary a great deal in length. In some specimens it is almost as big as the second, while in others, at the opposite extreme, it may be so short as to be hardly recognizable. In *Chelydra* there seems to be more constancy in the size of this rib, which is large enough to be easily recognized and apparently always so placed that it forms a rather inclined truss upon the proximal portion of the shaft of the second rib. In *Gopherus*, on the other hand, a series of variations much like those found in *Caretta* has been observed. In the extreme chelonian types, like *Amyda*, the first rib is always very short and displaced backward to such a degree that it forms a very powerful trusslike support for the second rib. In this latter case, the second trunk rib is pulled forward to extend upon the nuchal region, possibly to compensate for the marked

shortening of the first rib. A correlation may exist between the short length of the first rib and the absence of a costal plate for that rib. In all the species examined the short first rib always attaches itself to the costal plate developed around the shaft of the second costal cartilage.

There is certain evidence to show that the posterior displacement of the first rib is a function of the length of that rib. The evidence has been collected from a study of developing embryos of *Caretta caretta* and *Gopherus polyphemus*.

In *Caretta* (Fig. 21) embryos with a carapacial length of from 20.0 to 25.0 mm. the first rib may show a wide range of variability. At the one extreme it is so long that it might possibly develop its own costal plate and be quite like the second rib; at the other extreme it is so small as to be hardly visible. In the former case there is but little apparent displacement while in the latter case the shaft of the rib bends abruptly backwards to meet the second shaft. In specimen A. M. N. H. #4620 the first rib is almost as long as the second and is not displaced posteriorly. It develops a flangelike edge, which resembles the anlage of the costal plate of the second shaft. In specimens A. M. H. # 4605, 4623, 4619 and 4629 the first rib is but half the length of the second and converges toward the latter more noticeably than in # 4620. The flange is much reduced, being merely a roughened edge on the cranial and caudal faces of the shaft. In specimens A. M. N. H. # 4617 and 4618 the first rib is only one third as long as the second and is bent abruptly back to meet the latter. Again the flange is only a roughened edge. In each of these seven specimens the flange never gets out of its incipient stage of formation but its proximity to the larger flange on the shaft of the second rib causes it to fuse with the larger flange. Whether this would happen in the case of specimen # 4620 is an open question. It is possible, in this case, that had the embryo completed its full growth, the first rib might have developed a costal plate of its own. To continue the series, in specimens A. M. N. H. # 4627 and # 4659 the first rib is so small that it is not provided with any flangelike outgrowth of its own but immediately bends backward to attach itself to a slightly expanded portion of the flange of the second rib.

In specimen #4620 the scapula is not displaced to any abnormal position, as might be expected. It reaches the cranial surface of the first rib, where a small indentation in the anterior edge of the flange provides a recess to receive the tip of the scapular blade. Since all the specimens

referred to are of the same age and size, the differences described cannot be attributed to relative stages of growth and differentiation.

A series similar to the above has been observed in *Gopherus*. In this case, however, an additional stage has been discovered, one that illustrates

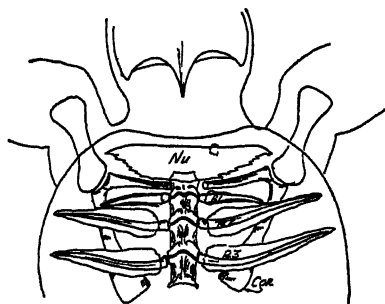


Fig 18

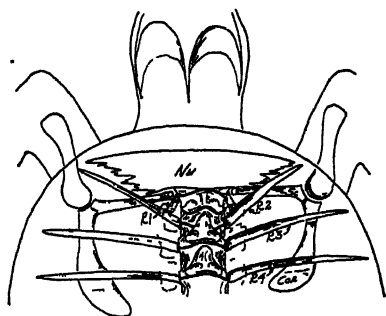


Fig 19

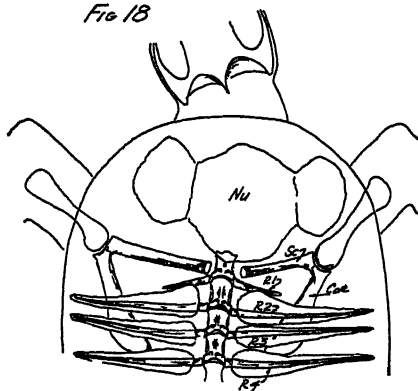


Fig 20

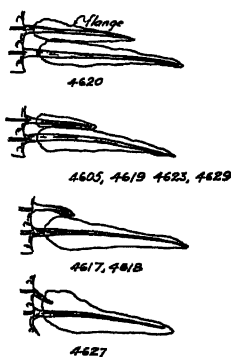


Fig 21

FIG. 18.—Shoulder region of a young *Carotta*.

FIG. 19.—Shoulder region of a young *Amyda*.

FIG. 20.—Shoulder region of a young *Pelusios* (Pelomedusidae).

FIG. 21.—Four stages in the evolution and variation of the first trunk rib in *Carotta*. A similar series was found in 10.0-14.0 mm. *Gopherus* embryos.

Abbreviations: Cor.—coracoid; Nu—nuchal plate; R1-R4—first to fourth trunk ribs; Sc.—scapula.

a still greater degree of reduction of the first rib. In fact, in this series the last specimen of the progressive stages possesses only nine ribs instead of the ten normal for *Chelonia*. From this we must infer that the scapula lies opposite its normal centrum, but the following vertebra is devoid of any lateral outgrowth that might be representative of a rib. The most anterior rib of the trunk series is evidently the normal second, for it is as large as a normal second, is attached to the proper numbered

vertebra and has developed a slight flange, as described for the ribs of *Caretta*. The variability of the size and persistence of the first trunk ribs is evident in another series of specimens in the author's collection of *Gopherus* embryos. In two instances specimens show on one side of the body ten trunk ribs and on the other only nine. The most anterior costal element on the side bearing the ten is very reduced and bent posteriorly at an acute angle. On the other side the corresponding rib is lacking altogether. A third specimen illustrates a case where one side of the body is provided with nine trunk ribs and the other with only eight. The most anterior element on the side where nine are present is not short or abortive but long like any second rib. On the other side the corresponding element appears not to have formed.

In all the above cases it is apparent that whatever displacement of the first trunk rib occurs, that displacement takes the form of a backward or posterior shifting of the axis of the rib and is somehow related to the length of the costal cartilage. In no instance has any definite displacement into an anterior position been observed except in adult specimens of *Dermochelys*. There may be a wide variation, however, in the degree of posterior displacement. In all specimens examined the scapula always seemed to remain in such a position that its dorsal tip was opposite the centrum of the vertebra directly anterior to the one to which the first trunk rib is attached. Even in those cases where there is no perceptible displacement of the rib, the scapula still occupies a place opposite to the centrum anteriorly adjacent to the one that bears the rib. It seems to the author that there is certainly no ontogenetic evidence to claim that the pectoral girdle got under the shell by any manner of posterior migration, a phenomenon so claimed by Watson. Moreover, it seems that the development and differentiation of the first trunk rib has nothing to do with the incorporation of the girdle within the shell.

Only in the Trionychid types of turtles is there evidence to support the hypothesis that the displacement of the anterior ribs contributes to the enclosure of the girdles. In this instance the displacement affects the second trunk rib, which in forms like *Amyda* is shifted so far cranial that its so-called sternal end comes to lie well in front of the shaft of the scapula. In this way the shaft of the rib cuts diagonally across the whole area occupied by the pectoral girdle. In some cases (*Amyda*) the third trunk rib may take part in the displacement process, but being originally well back in the trunk region, no matter what degree of displacement occurs, the sternal end of it is never carried so far forward

that it comes to lie anterior to the girdle region. This type of costal pattern is found only in the Trionychia; while in the Atheca, Pleurodira and the remaining Cryptodira, the second trunk rib is unaffected, or has its position changed so slightly that it contributes nothing to the mechanical enclosing of the girdle.

The reason for the appearance of the two patterns of the anterior trunk ribs is still uncertain. There may be a correlation between the fact that the Trionychids have a large nuchal and shoulder region that is relatively soft and unsupported by bony plates and the fact that these animals alone possess displaced anterior trunk ribs. The need for reinforcement in the vital nuchal region is evident. When the costal plates and nuchal dermal plates are large, much support is guaranteed, but when such support is greatly reduced or lacking, the adjacent ribs must replace the plates as supporting structures and secondarily shift their positions so as to accomplish this requirement. Since the first rib is so small and the scapula is directly anterior to it, it escapes being displaced; so whatever support the shoulder region desires must be obtained from the displaced second and possibly third ribs. Such a condition gives the erroneous impression expressed by Watson, that of the girdle having migrated internally under the shafts of the ribs.

THE PHENOMENA ASSOCIATED WITH THE DEPRESSION OF THE BODY

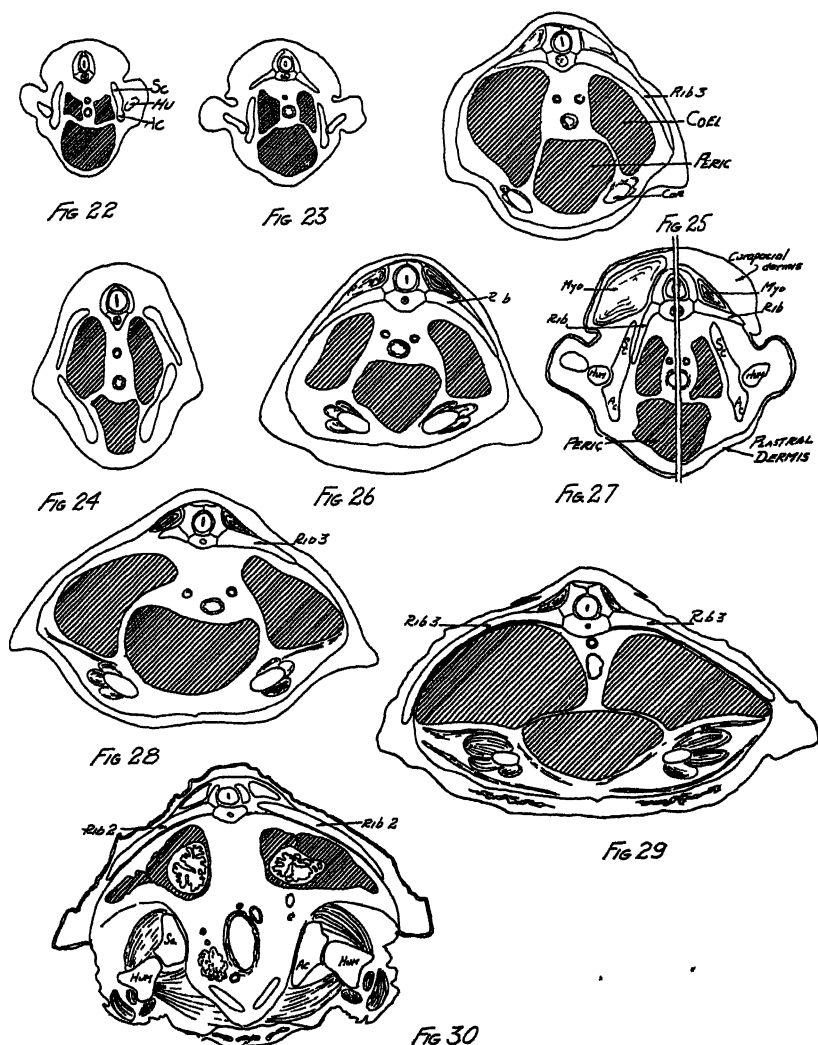
THE CHANGES IN THE COELOM SHAPE

Two changes in body organization are related to the flattening of the body and the enclosure of the girdles. These are associative factors rather than causative ones and affect respectively the form of the coelom and the disposition of the cartilage elements of the girdles. The former of these two is a rather important factor in so far as the peculiar changes in the contour of the coelom are apt to give the observer an impression that the pectoral girdle, at least, has progressively been pushed into the deeper recesses of the body. This conclusion would be an erroneous one, in view of the fact that all the evidence indicates that the girdle remains perfectly stable in its position and is merely overgrown by the lateral extensions of the body cavity.

In a series of embryos ranging from 8.0 mm. to 25.0 mm. the entire history of the coelomic changes can be worked out. Up to the 8.0 mm. stage, the chelonian body is much like that of any other generalized vertebrate, in that the body is much deeper than wide (Fig. 1). At

this time a cross-section of the body shows the right and left halves of the peritoneal cavity to be entirely dorsad of the pericardial cavity, while all three divisions of the coelom are yet mesad of the anlagen of the isomeric halves of the pectoral girdle (Figs. 22 and 23). Depression of the body is evident in the change in position of the right and left peritoneal cavities, which in a 10.0 mm. stage have begun to work their way ventrally between the pericardial chamber and the inner wall of the pectoral girdle, so that the pericardio-peritoneal septum (which hereafter will be designated merely as septum) no longer extends transversely across the body but dips slightly ventrally at its two lateral extremities. By the time the embryos have reached the 12.0 mm. stage (Fig. 25) the lateral limits of the peritoneal cavities reach laterally beyond the inner limits of the girdles and can be seen overgrowing the coracoid elements. The overgrowth is, of course, from the dorsal side. At this time the entire body cavity begins its regular posterior migration, with the result that the scapula no longer lies opposite any part of the coelom. At this stage, also, the septum is very obliquely placed in the body and the pericardial cavity is being enveloped by the peritoneal. As the changes progress through the 15.0 and 18.0 mm. stages (Figs. 26 and 28), the definitive shape of the animal becomes more pronounced. The elements of the pectoral girdle, which originally were laterad of the coelom, are now so placed that the greater part of the coelom is laterad of them. By the time the embryos have reached a 20.0 mm. stage the right and left abdominal cavities protrude well into the corners of the body under the now well-formed carapace. The septum is still somewhat oblique in its position but not as strongly so as in the earlier stages. By the time the animal has reached the 25.0 mm. stage, the final body proportions are assumed and are carried in toto into the fully formed young. The elements of the pectoral girdle are in a position equivalent to that in which they started, the scapula lying opposite the last cervical vertebra and occupying the relative spatial position to the underlying organs that it did in the earlier stages. The septum, while still adjacent to the coracoid, has once more flattened out and assumed a distinctly transverse position.

During all these changes the girdle, although overgrown by the coelom, never breaks through the coelomic epithelium to come to lie within the body cavity proper. There always exists a distinct and tough wall that separates the girdle elements from the adjacent peritoneal cavity. This wall, however, often bears slight depressions and indentures for the accommodation of the various pectoral muscles. Between the septum and



FIGS. 22-26, 28-29.—Series of diagrams illustrating the flattening of the body and its effect upon the coelom and the relation of the latter to the girdle. This is based upon the following forms: Fig. 22, a 7.0 mm. *Ohelydra*; Fig. 23, an 8.0 mm. *Ohelydra*; Fig. 24, a 9.0 mm. *Caretta*; Fig. 25, a 12.0 mm. *Ohelydra*; Fig. 26, an 18.0 mm. *Caretta*; Fig. 28, an 18.0 mm. *Ohelydra*; Fig. 29, a 25.0 mm. *Ohelydra*.

FIG. 27.—Composite diagram. Left half representing position of parts of pectoral girdle and rib in the generalized tetrapod (based on the organization of the parts of a chelonian body); right half representing the modifications of the body plan due to the presence of the enormous carapacial and plastral dermal layers and the incorporation of the rib and anapace, a condition found in all Chelonians with the possible exception of *Dermochelys*.

FIG. 30.—Cross-section through a 28.0 mm. *Ohelydra* in the region of the pectoral girdle, illustrating the manner in which the dorsal half of the body has grown laterally over the girdle, carrying the second trunk rib with it.

Abbreviations: Ac.—acromion process; Coel.—coelom; Cor.—coracoid; Hum.—humerus; Myo.—myotome; Peric.—pericardial cavity.

the inner wall of the bridge and plastron there develops a large mass of delicate mesenchyme tissue, which becomes highly vasculated.

All in all, the overgrowth of the parts of the girdle does give one an impression that the girdle has been squeezed into the deeper parts of the body and, unless the observer takes particular note of the constancy in position of the girdle, he is led to this conclusion. It is far better to use the change in shape and position of the pericardio-peritoneal septum as a criterion to determine what parts of the body have actually been displaced.

It is true, however, that certain elements of the pectoral girdle do assume new positions, but the change in position of the parts is in relation to one another and not to the surrounding organs.

The change in shape of the coelom in the region of the pelvis is not so pronounced as in the cranial portion of the trunk. The pelvic girdle encloses a much smaller portion of the body cavity than does the pectoral arch. Only craniad of the ilium and dorsal to the pubis can the coelom expand to any degree, and here it follows in all its minutiae the same procedure outlined in the preceding description. The absence of a pericardial chamber in the region of the pelvis simplifies the interpretation. If one studies cross-sections, the change from the circular pattern to the flat lunate type of coelom can be observed. Throughout the entire development, the girdle again remains free and distinct from the surrounding body cavity, being separated by a thin but tough peritoneal wall.

CHANGES IN SHAPE OF THE ELEMENTS OF THE PECTORAL GIRDLE

The second of the factors associated with the flattening of the body is that which controls the infolding of the elements of the pectoral girdle. In the following discussion the term girdle will be used to stand for the parts of the pectoral arch derived from the cartilage anlage. Since the dermal elements of the girdle do not enter into the scope of this paper, discussion of them can be terminated at this point. The only way in which the author satisfactorily succeeded in studying the cartilage girdle was to stain the animals in toto with toluidin blue and clear the objects entirely in synthetic oil of wintergreen according to the Spalttholz technique. In such preparations changes in the size and position of various parts can be followed step by step and the relationship of the parts to the surrounding softer organs may be interpreted, for all the organs remain in situ during the clearing process.

At the time that the mesenchyme has differentiated enough to permit the skeletal elements to be distinguished, the pectoral girdle appears well

up on the lateral side of the body, and just anterior to and somewhat dorsad of the much enlarged embryonic heart (Figs. 3 and 4). The parts distinguishable are the dorsal scapula, two ventral elements, an anterior spur, the acromion and a posterior process, the coracoid. These three parts are arranged in a tri-radiate pattern, which later in the development becomes more accentuated as the respective elements elongate. At first the acromion process is rather small and inconspicuous (Fig. 3), a condition that may be considered as recapitulating the degree of development of the process in *Triassochelys*. In the embryo this process protrudes from the cranial and ventral end of the scapula. It does not extend medially, as does the acromion of the adult, but lies more or less vertically on the side of the body almost in line with the axis of the scapula. Likewise the coracoid lies in the approximate lateral plane of the other elements of the girdle and is distinguished from the acromion by its more posterior position. In the early embryo the coracoid projects ventrally and posteriorly and does not fold under the abdominal viscera as does the adult coracoid. In all the specimens examined it was noted that the coracoid does not start out as a broad platelike structure, such as is found in *Triassochelys*, but appears as a blunt cylindrical process without a coracoid foramen. It seems that, as soon as this element and the scapula are laid down, they assume the form they will have in the adult; that is to say, there is little indication that they go through any recapitular stages except in so far as they arise in the very lateral wall of the body much as do the pectoral elements of more generalized reptiles. In the early stages of development the glenoid cavity is not easily seen but, when visible, it appears as a circular depression at the juncture of the coracoid and scapula.

As growth proceeds, the acromion and the coracoid elongate, the former more so than the latter, and the tri-radiate pattern of the three elements becomes more clearly defined. At this time (Figs. 4 and 5) the acromion, by virtue of its elongation, comes to have its distal end protruding somewhat anterior to the vertical axis of the scapula. However, the entire acromion body still lies in the lateral wall of the animal.

This stage is followed by a series the main trend of which is to produce an inbending of the coracoid and acromion processes. From their original position on the lateral walls of the body these elements eventually become folded under the venter of the body until they are finally almost parallel to the plane of the plastron. They are, therefore, no longer in the same lateral plane as the scapula, which was their position

at the start of their growth, but form decided angles with the axis of that organ, no matter from what aspect the girdle may be viewed.

The inward-bending of the two elements of the girdle appears to be associated with the flattening of the body. If we once more consider the rate of growth of the body and recall that the original deep body pattern is finally changed to a depressed body plan, it is evident that the lateral expansion goes on at a greater rate than does the dorso-ventral. This means, then, that if a structure is placed in a vertical position in the lateral wall of the body, as the girdle is placed, it is sure to be bent along its course at whatever point the greatest lateral pull is exerted. This point seems to be the region of the glenoid, the point where the coracoid and the scapula meet. If we consider now that the growth of the acromion and of the coracoid takes place from the proximal ends of these elements and that they elongate along certain definite lines at a rate more or less equal to the rate of the lateral growth of the whole body, we find that the distal ends of the coracoid and acromion nearly reach the mid-portion of the venter while the proximal portions around the glenoid region are being pulled laterally to quite some distance from the mid-line of the body. In this way the two sides of the pectoral girdle seem to be squeezed between the upper and lower shells of the animal. In a certain sense there is a sort of squeezing, since, if the girdles did not bend, the lower ends of the acromion and coracoid would eventually perforate the plastral plate. This not being desirable, these elements infold as the plastral plate flattens out. When once the infolding has started, it progresses at the same orderly rate as the plastron flattens, so that at various stages one can observe the gradual changes assumed in the angulation between the acromion, coracoid and scapula.

The degree to which the two lower parts of the girdle bend upon the scapula depends upon the degree of depression assumed by the adult animal. The more domed forms (*Terrapene*, *Testudo*, *Gopherus*) have acromion processes and coracoids that form obtuse angles with the scapula, while mediumly arched types (*Aromochelys*, *Emys*, *Chelydra*) exhibit about a ninety degree angle between the scapula and the ventral elements. In the flat species like *Amyda* the angle thus formed is acute, being a good deal less than ninety degree. This is a generalization but there are species that do not completely conform to the idea. In *Triasochelys*, according to Jaekel, there is more than a ninety degree angle at the glenoid region, in spite of the fact that the animal was apparently not a particularly high-arched form; the same condition exists today in

the Cheloniidæ and in *Dermochelys*, which must be considered as flattened types.

The changes in the composition of the pelvis need not hold the attention at this point since that topic was discussed in Part I of these studies in Chelonian Osteology. It need only be said now that the pelvis in some respects is more conservative in its changes than is the pectoral girdle, possibly due to the fact that it is the fixed girdle, and must persistently conform to the requirements of such a fixed girdle as is the case in other vertebrates. Nevertheless, in certain other respects it is more varied in its construction.

FOSSIL EVIDENCE BEARING ON THE PROBLEM

With the exception of only two forms, the body organization of all the Mesozoic Chelonia is essentially like that of our recent species. There is, therefore, little, if anything, to be gained for the purpose of this paper from the study of these.

The two forms that the author has in mind are *Eunotosaurus africanus* Seeley, which is believed by Watson ('14) to be ancestral to the Chelonia, and Jaekel's *Triassochelys duw*, which is the first authentic turtle from the lower Mesozoic. The former is a doubtful testudinate, although according to Watson there are some tendencies in body organization which seem to indicate a fairly close relationship between it and what might be considered the primitive plan of a chelonian. It seems that *Eunotosaurus* is the only possible link between the Chelonia and the primitive reptilian stock.

If it is accepted as being a prechelonian, then it shows a few interesting features that are similar to the stages in the ontogenetic history of modern forms. Chief among its peculiarities are its ribs. While these are in a somewhat dorsal position, like those described in a modern chelonian embryo, they are not horizontally displaced and do not fan out over the dorsal part of the ilio-sacral region. They apparently remain quite perpendicular to the vertebral column. This condition is almost identical to that found in an 8.0 mm. embryo of a living *Chelydra*. Although it is entirely possible that the developmental metamorphosis of the ribs of a living form recapitulates a series of stages that start with a form like *Eunotosaurus*, one discrepancy appears. In *Eunotosaurus* the last few presacral ribs, while not being displaced posteriorly, are actually articulated to the middle of their respective centra instead of to the line of union of two centra as they theoretically should be.

A second interesting similarity between *Eunotosaurus* and a modern chelonian embryo is that in each case the pelvic region is uncovered by the carapace. Unfortunately the ventral surface of the *Eunotosaurus* material that is known is in such a bad state of preservation that nothing can be deduced as to its original nature. If Watson's interpretation is correct, then the pelvic region in this animal was well marked off from the rest of the body, at least better than it is in recent species. If an extensive dermal carapace existed in *Eunotosaurus*, it is hardly possible that it could have elongated to the length necessary to cover the pelvic region without causing a horizontal displacement of the presacral ribs.

When the condition of its ribs is considered, it is entirely possible that *Eunotosaurus* did not have a carapace. Yet there is evidence of the presence of dermal bone in the form of fragmentary discs on the dorsal surface of the animal. Fragmentary as these are, they are distinct enough to indicate a certain bone-developing influence in the carapacial layer. It is also possible that the fossils as found represent individuals that have not completely developed and so have not formed a complete carapace. Watson particularly notes that the body of *Eunotosaurus* is deeper than wide, a feature so characteristic of the early embryonic stages of recent chelonians.

The construction of the scapula may indicate the degree to which the carapace may have formed and functioned. While in all other fossil Chelonia the scapula is cylindrical, that of *Eunotosaurus* is distinctly broad and flat. The cylindrical scapula is always associated with a pyramidal type of musculature, which develops in the Chelonia because the ribs do not form the satisfactory surface of attachment for muscles of any other form. A triangular scapula is not associated with a pyramidal form of musculature. This fact may indicate that the carapace was only in its incipient stages of development in *Eunotosaurus* and had as yet not developed to the degree where it had eliminated the superficial musculature by extending over the sides of the body.

Triassochelys (Jaekel '16) is so like the modern chelonian that its skeleton contributes little to the present problem. The only feature that is at all striking is the persistence of cervical ribs. Phylogenetically these become reduced and disappear in the other Chelonia. It may be that the tendency to atrophy ribs in this way may be carried from the cervical region into the trunk region, where it has been shown that at least the anterior rib remains small and may in some cases actually dis-

appear (c. f. *Caretta* and *Gopherus*, pp. 106-108). In the embryology of recent species the atrophied remains of cervical ribs are quite recognizable although they never complete their development to persist in the adult.

The carapace and plastron of *Triassochelys* are so well developed that they give no hint as to the stages leading up to their formation or their influence upon the nature of the girdles or the modification of the latter due to enclosure.

SUMMARY AND CONCLUSIONS

There is so little fossil evidence of ancestral Chelonia that problems dealing with the phylogenetic history of the order have to be worked out from the developmental history of recent species.

Eunotosaurus may be ancestral in the light of apparent similarities existing between it and the early developmental stages of recent Chelonia.

The enclosure of the girdles within the shell is a result of several growth factors acting in conjunction with one another; these bear a certain causal relationship to one another.

The dynamic process by which the girdles are enclosed within the shell are as follows:

a) The body grows more rapidly in lateral diameter than it does in dorso-ventral and thus becomes flattened.

b) The carapace with its peculiar mode of growth is probably the cause of the flattening of the body.

c) Any skeletal parts connected with the carapace will be compelled to follow a plan of growth similar to that affected by the carapace.

d) The ribs are connected very early with the inner wall of the carapace.

e) They are prevented from growing in a normal dorso-ventral direction and are carried far laterally and dorsally by the carapace.

f) The shafts of the ribs never extend ventrad to the dorsal ends of the girdles at the time that the ribs become associated with the carapacial dermis. Therefore the girdles never come to lie outside of the ribs.

g) The growth of the carapace over the pelvis carries the ribs with it, so that they eventually form a fanlike cover over this region.

h) In some species (*Amyda*) there is a tendency for the anterior trunk ribs to shift forward to cover over the shoulder region much as the presacral ribs cover the pelvic girdle.

i) There has been no apparent movement of the girdles within the shell. The shell appears to grow around the girdles and thus to enclose them.

j) The flattening of the body has caused the coelom to be squeezed far laterad of the girdles, but the latter structures have not been pushed internally.

k) The pectoral girdle has been folded so that it will fit with greater snugness between the carapace and plastron.

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Dedicated to

GEORGE B. DORR,

lover of Nature, and creator of Acadia National Park.

THE SCENERY OF MT. DESERT ISLAND: ITS ORIGIN AND DEVELOPMENT *

By ERWIN J. RAISZ

	Page
Introduction	124
Location	125
Relief	125
Physiographic Divisions	127
Soil	128
Climate	128
Vegetation	128
Inhabitants	128
Lafayette National Park.....	129
Nomenclature	129
Previous Geological Work.....	129
Acknowledgments	130
The Geological History of Mount Desert Island.....	131
The Constructive Period.....	131
The Forming of the Weak Rocks.....	131
The Basic Rocks.....	132
The Granitic Intrusion.....	133
Folding and Fracturing	133
Later Intrusions	134
The Continuity of the Trap Sheet over New England.....	135
The Great Denudation.....	136
The Erosion.....	136
The Jura-Cretaceous Peneplane	136
The New England Peneplane.....	138
Is the New England Peneplane of Marine Origin?.....	138
The Probable Explanation of the Presence of Mount Desert Mountains	139
The Uplift and Dissection of the New England Peneplane.....	140
The Ice Age	141
The Upper Marine Limit.....	144
Review of the Literature.....	144
The Cliffs of Mount Desert Island.....	145
Giant Steps and Chasms.....	146
The Tilted Rock.....	147
The Cadillac Cave.....	148
Beach Deposits and Delta Deposits.....	149
Fossils	150
Washed Surfaces.....	150

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	Page
Features Due to Glacial Erosion.....	154
The Glacial Troughs.....	154
The Lakes.....	155
The Asymmetry of the Mountains.....	156
The Trend of the Topography.....	159
The Question of Local Glaciation.....	159
The Question of Multiple Glaciation.....	161
The Potholes.....	161
The Saddle Ponds.....	162
Glacial and Other Deposits.....	163
The Glacial Deposits of Mount Desert Island.....	163
Fluvio-Glacial Deposits.....	163
The Delta Deposits.....	164
The Unstratified Till.....	165
Other Deposits.....	165
The Blue Clay.....	165
The Surface Drift.....	165
Post-Glacial Soil of Weathering.....	166
Talus Slopes.....	167
Erratics.....	167
Shoreline Development.....	168
Shoreline of Submergence.....	168
The Shoreline on Granite.....	168
The Baker Island Type of Shoreline.....	168
The Thunder Hole Type of Shoreline.....	171
The Weak Rock Shoreline.....	172
The Shoreline of the Contact Zone.....	172
The Coves.....	175
Beaches, Bars and Tombolos.....	176
Spits and Bars.....	177
Cuspate Bars and Tombolos.....	178
The Drainage History.....	179
The Divides.....	180
The Lakes.....	181
Post-Glacial Stream Notches.....	183
Drainage Modifications.....	183
Future Development.....	184
Bibliography.....	185

INTRODUCTION

On September 5, 1604, a small open boat sailed along the unknown waters of the new French province, Acadia. It had left St. Croix in the morning, and on the wings of the fresh breeze had advanced far to the southwest along the coast. There were fourteen men in the boat, and their commander was the famous navigator, Samuel Champlain.

The coast along which they sailed was a rocky archipelago, with deep bays and peninsulas full of islands and perilous ledges. The land was covered with heavy forest. It was surprisingly low for its rugged character. Nowhere was the general elevation more than a few hundred feet.

At sunset suddenly a bold mountain range appeared in the west, apparently rising directly from the sea. Here the explorers landed. After closer examination on the following day, they found that the mountains formed the backbone of an island roughly circular in shape, ten miles across and separated only by a narrow channel from the mainland. The range ". . . is very high and notched in places, so that there is the appearance to one at the sea of seven or eight mountains extending parallel with each other. . . . The summit of them is destitute of trees, as there are only rocks upon them." Thus writes Champlain and accordingly he named the island "Isle des Monts Deserts."

The "Island of the Barren Mountains" proved to be the largest island of the Gulf of Maine (100 square miles) and the loftiest piece of land along the Atlantic coast of the United States (1527').

LOCATION

Fig. 1 shows the location of the Island, in the physiographic province known as the "New England Upland." If we take into consideration the part of this province which is submerged under sea level at the present time, Mount Desert Island is nearly in the center of it, midway between the mountains on the Canadian border and the Newfoundland Banks. It is suggested that in order to follow the discussion with full understanding, the reader have before him the Lafayette National Park topographic sheet, published by the United States Geological Survey and bearing on its reverse side an account of the geology of Mount Desert by George M. Wood.

RELIEF

The Island is composed of a central granitic mass nearly circular in shape and surrounded on all sides with older and weaker rocks.

In physiographic terms the surface of the Island forms parts of the New England peneplane,* and the central mountainous mass is an

* If erosion acts upon a region for a sufficiently long time, it finally wears down the land to an undulating lowland near sea level. Such a lowland was termed by W. M. Davis a "peneplain" (almost a plane), later spelled by Johnson "*peneplane*." Hills or mountains left standing above the peneplane are called "monadnocks" after Mount Monadnock in New Hampshire.

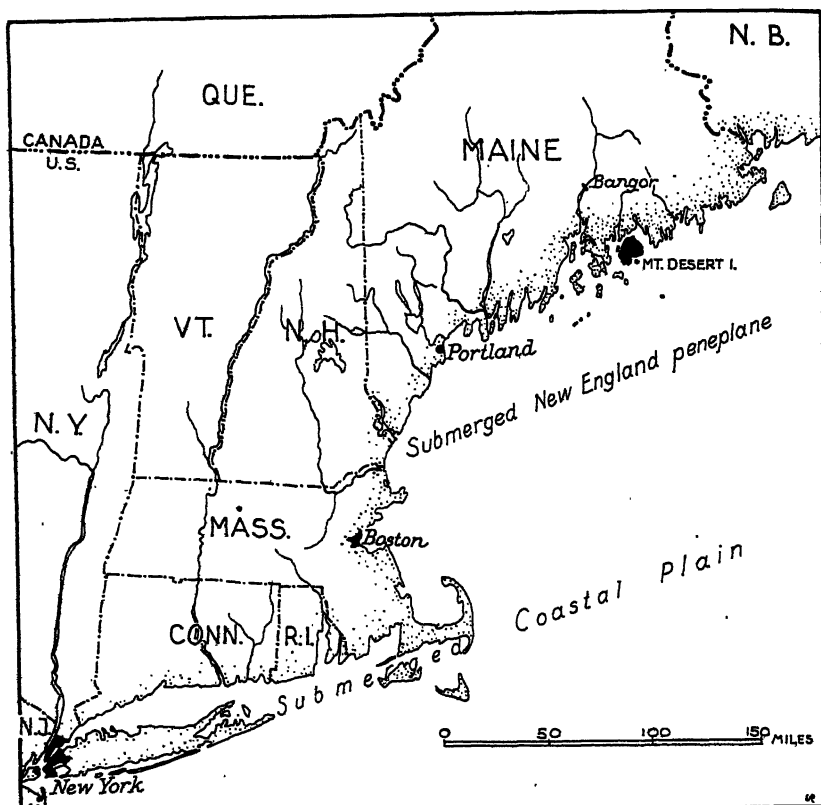


FIG. 1.—Location map of Mount Desert Island.

erosional remnant or "monadnock" on this peneplane. The presence of the mountainous monadnock is due to difference in rock resistance. The central granitic mass was able to withstand the general leveling which wore down the surrounding country to a peneplane. The bevelled land was slightly uplifted, dissected into low hills and valleys, then submerged under sea level. The submergence of this rolling country accounts for the highly irregular shoreline with its countless islands and peninsulas.

Before the Ice Age the monadnock was a single east-west trending ridge. During glaciation this ridge was cut across by ten parallel north-south trending glacial troughs. These troughs are so deep and steep-sided that the ridges between them appear as separate mountains. In most of the troughs are beautiful lakes. One is carved below sea level; this is Somes Sound, which cuts the Island nearly in two in the middle.

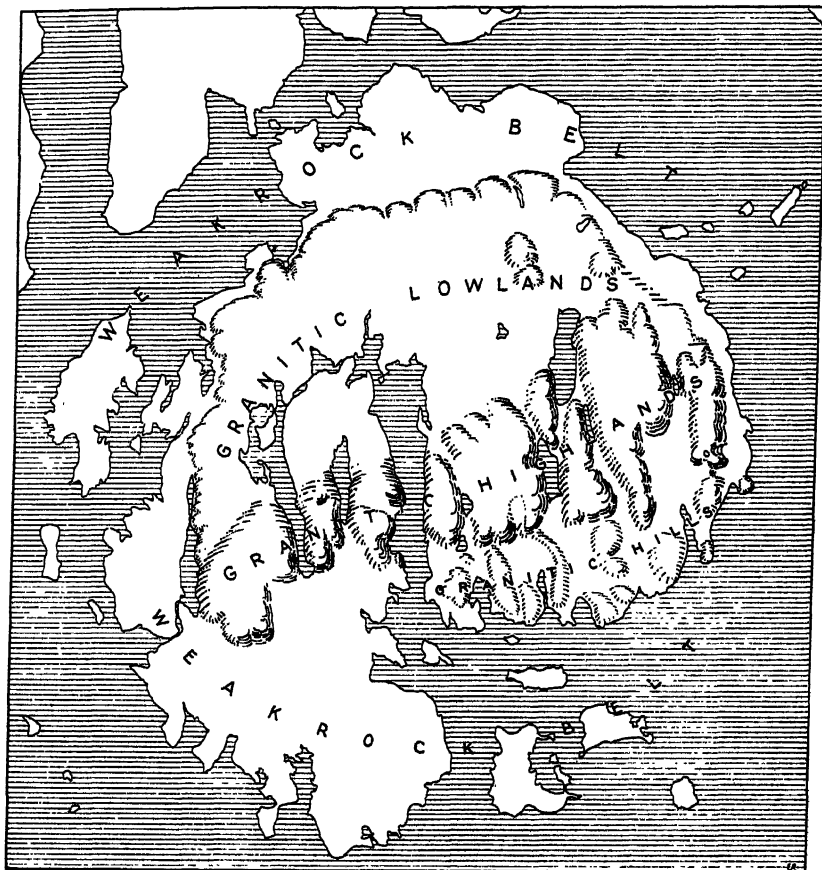


FIG. 2.—Physiographic divisions of Mt. Desert Island.

If the sea level were a few feet lower, Mount Desert Island would be a peninsula. If the sea level were a few hundred feet higher, the lowlands would be covered completely by the ocean and the monadnock would stick out as a most picturesque group of islands.

PHYSIOGRAPHIC DIVISIONS

Not all of the central granitic area stands out as a monadnock. The peneplanation advanced far enough to level off about half of the granite. In the northern part of the Island the granite seems to be of as resistant a quality as that in the mountains, but the land is low. This granitic lowland is still higher than the surrounding weaker rocks from which it is separated by a low rim or scarp.

The southeastern part of the granitic mountains, possibly because of some structural reason, is lower and has a different appearance, and is referred to in the later discussions as the "granitic hills."

We thus have four natural divisions of the Island (see Fig. 2):

- 1) The granitic mountains
- 2) The granitic hills
- 3) The granitic lowlands
- 4) The weak rock lowlands

SOIL

The Island is in part covered with a sheet of glacial debris, very unevenly distributed. The mountain tops are nearly barren, but in the valleys there are great accumulations of material. There is also some residual soil on the Island derived from postglacial weathering of the bedrock.

CLIMATE

The climate of the Island is generally mild, with an average July temperature of 64°; a January temperature of 24° and an average annual temperature of 43°. The prevailing wind is from the northwest. The annual precipitation is 42 inches, fairly evenly distributed throughout the year.

VEGETATION

The moist climate, together with fairly fertile soil, favors a great abundance of vegetation at the lower levels. There heavy forest and thick underbrush make exploration of the Island very difficult. The forest cover conceals the smaller land forms, as cliffs, terraces, eskers and other glacial forms. On the other hand, differences in vegetation often indicate differences in the rock beneath.

INHABITANTS

There are about 7000 permanent inhabitants on the Island, approximately half of them in the town of Bar Harbor. The occupations of the scant original population were farming, fishing, lumbering and quarrying. Now the chief source of income is from the summer visitors. The population in summer is estimated to be from two to three times that in winter.

A good system of roads and a splendid system of mountain trails and foot-paths are maintained. Some of the most valuable information was obtained from cuts along the roads. The numerous quarries on the Island were also very helpful.

LAFAYETTE NATIONAL PARK

The beauty of mountain, lake and shore, a favorable climate and nearness to great centers of population attract many people. Mount Desert Island became a fashionable summer resort early in the second half of the nineteenth century and the popularity of the Island has steadily increased.

Through various gifts, due to the interest and energy of Mr. George B. Dorr, a member of one of the earliest summer-resident families upon the Island, the main part of the Island's beautiful mountain chain has been set aside as a playground of the nation, under the name of Lafayette National Park.* This is the first national park established east of the Mississippi River.

NOMENCLATURE

The names of a number of the mountains were recently changed by the National Geographic Board upon the establishment of the Park. This new nomenclature appears on the United States Geological Survey maps and recent charts of the United States Coast and Geodetic Survey. These names are here used, the former names being given in parentheses.

The changes are indicated in the following table:

<i>Old Name</i>	<i>New Name</i>
Newport Mt.	Champlain Mt.
Dry Mt.	The Flying Squadron
Green Mt.	Cadillac Mt.
Jordan Mt.	Penobscot Mt.
Little Browns Mt.	Parkman Mt.
Browns Mt.	Norumbega Mt.
Robinson Mt.	Acadia Mt.
Dog Mt.	St. Saveur Mt.
Western Mt. East Peak	Mansell Peak
Western Mt. West Peak	Bernard Mt.

The village of *Somesville* appears on the U. S. G. S. maps as *Mt. Desert*, the name of its post office.

PREVIOUS GEOLOGICAL WORK

Several of our most prominent geologists have visited the Island in past years and published the results of their investigations. One of the earliest papers dealing at some length with the geology of the Island is

* Since the writing of this paper the name of the park was changed by Act of Congress from Lafayette National Park to Acadia National Park.

W. O. Crosby's "Geology of the Frenchman Bay, Maine" (9)* which describes the outstanding geological features in a most satisfactory way.

The most extensive study of the Island was made by Nathaniel S. Shaler. His results are published in the Eighth Annual Report of the United States Geological Survey, Part 2, 1886-87 (25). He prepared a geologic map of the island, studied the surface deposits, and worked out the geological history. While some of his views are not now held, his book is still, forty years after its publication, our chief source of information on the geology of the Island.

G. H. Stone in his great work on "The Glacial Gravels of Maine and their Associated Deposits" (U. S. G. S. Monograph 34) does not treat of Mount Desert Island very extensively, but his information on the adjacent region is of much value to any worker in the region (27).

Professor William Morris Davis published a chapter on geology in the "Flora of Mount Desert Island" by Rand and Redfield (14). This paper is intended for the general public and makes wonderfully clear, even for the untrained reader, the principal geological events in the history of the Island.

A short paper by Florence Bascom (4) presents a brief but fairly complete picture of the local geology.

Professor H. L. Fairchild in his "Postglacial Uplift of New England" (17) uses the Island as an illustration of his postglacial emergence theory.

Professor Douglas W. Johnson in his "New England-Acadian Shoreline" (21) gives the most detailed study of the physiography, with the most original views upon the coastal features of the Island. The present paper is largely a study of the problems raised by Professor Johnson's book.

There are several shorter articles referring to the geology and the physiography of the Island, but most of them use one or another of the works above cited as a source of information.

ACKNOWLEDGMENTS

The present study is the result of a summer's field work in 1926, made possible by the courtesy of Mr. George B. Dorr, creator and superintendent of Lafayette National Park, who covered the author's field expenses and at all times rendered the most generous aid. The work has been

* Throughout this paper the bibliographical references are designated by an italicized number in parentheses. The reader is referred to the Bibliography at the end of this paper for their elucidation.

carried on under the direction of Professor Douglas Johnson of Columbia University to whom the author is indebted for valuable criticism and advice. Both in the field and in the office Professor Johnson gave the author the benefit of his wide experience. Two park rangers, William B. Campbell and Orient Y. Thompson, accompanied the author in most of his field work and proved to be understanding and helpful guides and companions. The author wishes to thank Mrs. L. Hugentobler, Miss B. Blauvelt and Miss G. Hargrave for their help in getting the manuscript into final form for publication.

If, despite all the help the author has received, there remain in the text phrases which fall strangely upon the American ear, it is hoped that the reader will prove indulgent toward one who has not yet fully mastered the language of his adopted land.

THE GEOLOGICAL HISTORY OF MT. DESERT ISLAND

Mount Desert Island as it stands today is a result of all the processes and forces operating on it in the past. The best understanding of the present features can be obtained by tracing its geological history. The following outline will serve to summarize events which will be elaborated in the following chapters. As the author in his study necessarily restricted himself to the field of physiography, the petrographic facts here given are based largely on Shaler's work.

The history of the Island can be divided with some generalization into three epochs, very unequal in duration:

1. The *constructive period*, which includes all the time, up to the early Mesozoic, during which the rocks of the Island were being formed.
2. The *great denudation* to the end of the Tertiary, when erosional processes dominated.
3. The *Ice Age*, during which the land forms attained their present appearance. The relatively short post-glacial time is here included.

Although these periods may be related in duration of time somewhat as 100:10:1, their relative importance in the sculpturing of the present land forms is rather in reversed proportion.

THE CONSTRUCTIVE PERIOD

THE FORMING OF THE WEAK ROCKS

The first important event in the history of the Island was the formation of the extremely complex series now constituting the peripheral belt of weaker rocks. Generally there are more schistose formations

west and south, more flagstones and shales on the north and east. They are not easy to identify because of subsequent igneous intrusions, which affected these rocks profoundly. Certainly they do not represent a single period of deposition and are probably of very different age. The "sedimentation-uplift-peneplanation" cycle has been repeated perhaps several times. But because the sequence of the beds has not been worked out with certainty, and further because from the physiographic point of view such sequence is not important, these rocks are treated here as one series. The general term "weak rocks" is used for all pre-granitic rocks, which are differentiated by Shaler into the Bartlett Island, Schooner Head, Bar Harbor, Cranberry Island and Sutton Island series.



FIG. 3.—The weak rock series. Schistose rocks on the west and sediments on the east, both indurated by basic igneous intrusions. The peneplane between the schist and sediments is hypothetical.

The age of the weak rock sediments is not known, but they may be Pre-Cambrian. No fossils are found, even where the rocks are least disturbed. Similar rocks found in Penobscot quadrangle are thought to be early Paleozoic (*6-map*).

THE BASIC ROCKS

The history is complicated by periods of vulcanism developed on a vast scale, and perhaps repeated in widely different ages. The sediments were extensively penetrated in places by igneous rock, mostly of basic composition. It is often impossible to tell where the igneous material ends and where the sediments begin. The igneous rocks are a confused mixture of intrusive sheets, lava flows, breccias, tuffs, while several systems of dikes can be differentiated. These rocks have one character in common, which is most important from a physiographic point of view: all offer only moderate resistance against erosion.

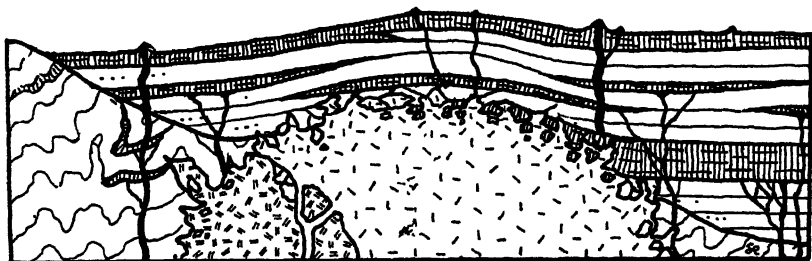


FIG. 4.—The granitic intrusion. Note the irregular contact, with penetration and incorporation effects.

THE GRANITIC INTRUSION

The most important event in the history of rock-making was the great granitic intrusion. The molten mass forced its way through the older rocks, partly uplifting them, partly melting and incorporating great chunks of them. The whole mass crystallized into a coarse hornblende-biotite granite.

Though less complicated than the earlier basic intrusions, the granitic rocks are not of uniform character. The borders of the granite are gray whereas the general mass is pink, while in the western part of the Island the granite passes into gabbro-diorite.

The granitic mass of Mount Desert Island is not an isolated occurrence. As shown on the map by T. Nelson Dale (*12-map*), it is a part of an extensive intrusion or batholith which extends from New Brunswick to Penobscot Bay. (The granites south of Penobscot Bay are younger.) This granite mass crystallized deep below the older rocks, and the roof or ceiling of older rocks was very irregular, with masses of the roof extending down into the granite, and "cupolas" of the granite projecting up into the roof cover. Erosion was not able to reach the granite everywhere, hence only the more outstanding cupolas are stripped of their old rock cover. Such a cupola is Mount Desert Island. The continuity of the granite below is testified to by the granitic dikes and patches in the weak rock belt.

The age of the granitic batholith is thought to be early Devonian. Granitic pebbles are found in the late Devonian Perry formation in eastern Maine, while such pebbles are absent in the Silurian formations (*26-p. 20*).

FOLDING AND FRACTURING

There were doubtless mountain-making periods before the granitic intrusion. Presumably also there was a great amount of earth move-

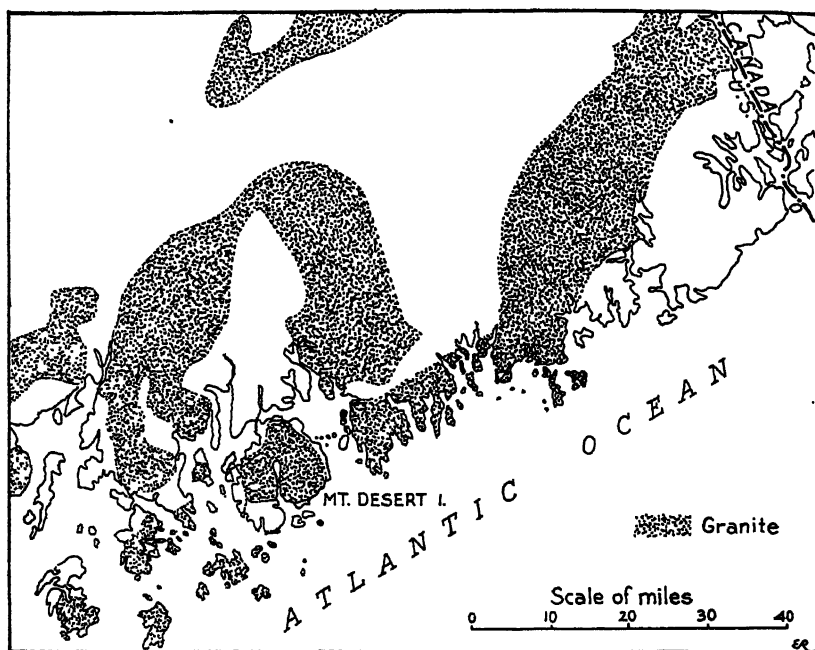


FIG. 5.—Map of Eastern Maine showing distribution of the granite (after T. Nelson Dale). Mt. Desert may be a "cupola" of the big Maine batholith.

ment during the granitic intrusion, and certainly important disturbances occurred after the granitic masses had cooled and crystallized.

During these earth movements the sediments and associated basic igneous rocks were thrown into open folds, anticlines and synclines. The igneous rocks were cracked into a mesh-work of joints, in addition to the original columnar jointing which characterized some of them. The flagstones and schists were cracked into minute prisms. The big mass of granite offered more resistance. By its nature folding was not possible. Most probably it suffered torsional stresses and a joint system developed with vertical master-joints trending S 20 E, dividing the granite into huge blocks. There was also occasional movement along the joint planes producing faults.

The last great disturbance is probably to be correlated with the Appalachian Revolution at the close of the Paleozoic period. It is believed that at this time the region was lifted high above sea level.

LATER INTRUSIONS

Into the north-south (S 20 E) cracks igneous material was forced, crystallizing as a light pinkish, fine-grained feldspar-quartz material.

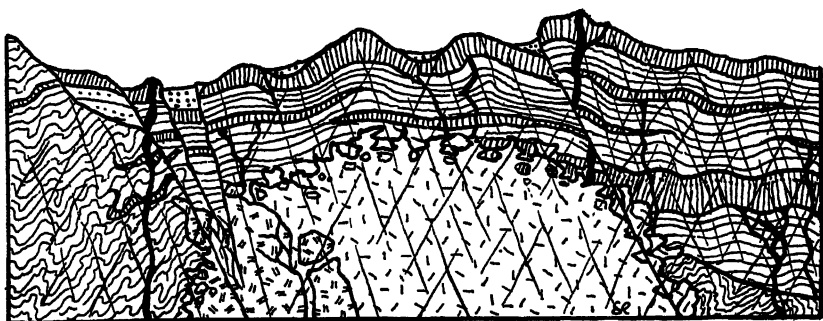


FIG. 6.—The postgranitic disturbance, showing folding, fracturing and faulting of the rocks.

forming the "pink dikes." These dikes are common in the granite, but not very apparent because of their similar color. In spite of the abundance of quartz, they are not resistant against erosion because of their prismatic joints and brittle character.



FIG. 7.—The dikes and the lava flows which probably covered much of the surface. The dikes are parallel (nearly N-S) and rather evenly distributed.

More apparent are the dark diabase dikes. These are 2 to 20 feet thick, and their direction is so uniformly S 20 E that they can be used with fair certainty as a compass. The diabase dikes are less resistant than the granite, and exerted a great influence in directing stream erosion, and later that of ice. Their distribution is surprisingly uniform. There is scarcely a stretch of a mile on the Island where at least one cannot be found. These dikes are also present in the older rocks, but because of similar color and the presence there of older dikes, they are not so evident.

THE CONTINUITY OF THE TRAP SHEET OVER NEW ENGLAND

The size, color and texture of the diabase dikes as seen in the hand specimen are just the same on top of Cadillac (Green) Mountain (1532

ft.) as at sea level. We have to assume the dikes extended a long way upwards. They may even have reached the surface, forming lava flows. The presence of abundant trap material in the highest mountains midway between the extensive trap sheets of the Bay of Fundy and of the Connecticut Valley is significant. Possibly we find here some support for the theory of a former continuity of the trap flows over much of New England.

The dikes represent the last important rock-building process on the Island. By analogy with similar occurrences they can tentatively be assigned to the Triassic period.

There was a still later effect: a filling of the cracks with green epidote vein material. With this closes the constructive period of the region. Smaller disturbances occurred in later times, and the diabase dikes are often displaced. But the later earth movements of importance were of a regional (epeirogenic) nature.

THE GREAT DENUDATION

THE EROSION

Erosion naturally occurred whenever the region rose out of the sea, and perhaps was at the maximum at times when the mountains were highest; but it was not always the *dominating* process. When the constructive process ceased, erosion became the dominating process, and has remained so up to the present time, except during occasional periods of regional uplift.

We have to assume that at the close of the Constructive Period there existed above the present mountain tops several thousand feet of granite, a great mass of older rocks, as well as later dikes and possibly flows of trap.

The rain and rivers slowly wore down the mountains, until the less spectacular but untiring erosive processes had destroyed much of the work accomplished by the mountain-making processes. "*Gutta cavat lapidem, consumitur annulus usu.*" The lava flows, if there were any, are swept away; gone are all the old rocks above the granite; and erosion has bitten deep into the granite itself. The same prolonged erosion at first deepened valleys, then broadened them, and after passing through the young, mature and old stages of the river erosion cycle, produced a low undulating plain near sea level—a peneplane.

THE JURA-CRETACEOUS PENEPLANE

There are many indications in the eastern United States that the mountains of the Appalachian Revolution were worn down to a pene-

plane in the Jurassic period or at least by early Cretaceous time. This is not the New England peneplane but an older level, which appears now only along the Fall Line and supposedly on the top of certain mountain ranges (*3*).

The lowlands of Mount Desert Island are a part of the New England peneplane, often called the "New England Upland" because inland from the coast it rises high enough to give a plateau-like upland. If there was an earlier peneplane than the New England, traces of it might be found on the Mount Desert mountains. Did the granitic mass of Mount Desert Island resist at this earlier time the general peneplanation, and stand out as a monadnock; or was it worn down to the same level as the surrounding country? In the latter case, are traces of the older peneplane preserved? These are open questions.

There are some indications in favor of the view that traces of the older Jura-Cretaceous peneplane are preserved. Looking over the flat tops of the mountain ranges we find that they show a certain accordance of elevation. (Sargent Mt. 1344', Pemetic Mt. 1262', Cadillac Mt. 1532', Flying Squadron (Dry) Mt. 1268', etc.) Furthermore, the biggest mass of mountains in the center (Sargent Group) has not the highest elevation, as we might expect to be the case if erosion had been the only process at work on homogeneous material in one cycle. Although the flat tops of the single ridges might be explained by planation of the over-riding ice sheet, the accordance of elevations together with the evidence of the Sargent Group indicate that there was an old peneplane surface not far above the top of the present granitic mountains. Perhaps this level was the ancient Jura-Cretaceous peneplane.

Near the end of the Mesozoic the Atlantic coast was uplifted and a new cycle of erosion was initiated.

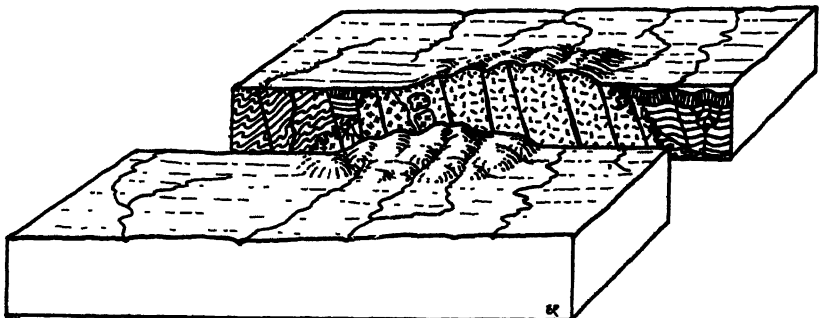


FIG. 8.—The New England peneplane with Mt. Desert range rising as a monadnock above it. There may have been an earlier peneplane at the height of the mountain tops.

THE NEW ENGLAND PENEPLANE

If we connect the ridge crests and the hilltops of New England (disregarding the valleys as the results of later dissection), we get a gently undulating plane, with occasional isolated mountains rising sharply above it. This plane bevels all kinds of geological structures, and is called the New England peneplane. The region around Mount Desert Island is a part of this peneplane and the Mount Desert mountain range is a monadnock on it.

IS THE NEW ENGLAND PENEPLANE OF MARINE ORIGIN?

Barrell (3-pp. 407-428) suggested that the New England peneplane was not eroded by rivers and rain, but was carved by the waves of the ocean. His evidence consisted chiefly of supposed terraces found in different parts of southern New England. He did not state the height of the terraces at Mount Desert Island and they can be projected only with due allowance for possible local disturbance.

If these terraces really exist and are of marine origin, there is no better place to see them than on Mount Desert Island, which was more exposed to prolonged action of the waves than places now farther inland. Before Barrell undertook his study, Shaler found a number of benches on the Island which he thought to be of marine origin. But a comparison of Barrell's figures for terrace heights with those of Shaler appears to show nothing more than occasional fortuitous agreements, as indicated in the table herewith:

Terrace levels as described by:

Barrell in southern New England at the head of the terraces	projected to the Connecticut shoreline	Shaler on Mt. Desert Island
120	120	90
240	240	165-185
400	400	220-240
540	530	270-290
740	680	300
940	800	380-430
1140	1000	480-500
1380	1200	?
1720	1450	?
		?
		1000
		1140-60
		1210-40
		1280-1320
		1460-80
		1510

Both Shaler and Barrell give wide limits of variation for the altitudes of their terraces. The uncertainty of Barrell's figures is still further increased by projecting them so far from the areas of his study. Furthermore, at both places the supposed terraces lie very close to each other. Under these conditions an apparent agreement of the figures would in no case be conclusive.

The author made a careful investigation of the supposed marine benches of Mount Desert Island. The result, unfavorable to the marine theory, will be discussed in a later chapter.

There is some direct evidence for the non-marine origin of the New England peneplane: Mount Desert Island is a nearly circular granitic area surrounded on all sides by weaker rocks. Had the peneplane been carved by waves, the main attack must have come from the south, and the mountain monadnocks, as remnants left by incomplete marine erosion, should be more toward the northern side of the granitic area. As a matter of fact the monadnock mass is nearer the southern margin.

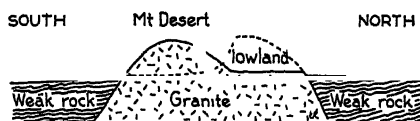


FIG. 9.—The actual position of the Mt. Desert monadnock in relation to the extent of the resistant granite area (solid line). If the New England peneplane had been carved by waves, the monadnock should be on the northern side of the granitic area, as indicated by the broken line.

(Fig. 9). Barrell's theory of the marine origin of the New England peneplane appears to find no support on Mount Desert Island.

THE PROBABLE EXPLANATION OF THE PRESENCE OF MOUNT DESERT MOUNTAINS

There are in eastern Maine hundreds of square miles of granite most of which was very well peneplaned. The question arises: Why were the Mount Desert mountains able to resist erosion?

The explanation may lie in the peculiar position of Mount Desert Island, shown on the map, Fig. 5. The granite cupola of Mount Desert Island is surrounded on all sides by a broad belt of weak rocks, and these weak rocks diverted the large rivers coming from the north. Only the small rivers originating on the granite itself carried out the work of erosion upon the mountains, naturally at a slower rate. A repetition of similar conditions is found on Isle de Haut in Penobscot Bay.

Another possibility is that the original mass of granite was here higher than at any other place in the region. Thus Mount Desert Island might be the high part of a high cupola.

A third possibility, and perhaps the most probable, is that differentiation of the granite resulted in areas of varying resistance, and that the Mount Desert range represents a phase of peculiar durability. The test of this theory is not simple, because variable degrees of weathering in collected samples of the rock may be due to purely local causes, and afford no evidence as to the behavior of large masses; nor is hardness of a hand specimen any criterion as to the resistance the same rock will offer to long-continued weathering and erosion. It can only be said that there do exist marked differentiation phases of the granite, and that, for example, a finer gray facies is fairly widespread in parts of the granitic lowland, whereas the granite of the high mountains is prevailingly coarser and of a color varying from red to pinkish gray. On the other hand, finer gray granite is found in the mountains and coarse red granite in the lowlands. Only a detailed petrographic study of the whole area, such as lay beyond the scope of the author's study, would solve this problem.



FIG. 10.—The uplift and dissection of the New England peneplane.

THE UPLIFT AND DISSECTION OF THE NEW ENGLAND PENEPLANE

After the New England peneplane was formed the whole region was uplifted and tilted to the southeast. The sluggish rivers were rejuvenated, and the peneplane was redissected into hills and valleys. This period of dissection could not have been extremely long, because the rivers in the Mount Desert region did not pass beyond the sub-mature or mature stage of development. It succeeded, nevertheless, in lowering the average level of the weak rock belt somewhat below the granitic lowlands.

The same dissected character of the surface can be traced by soundings far out in the sea. The shoreline was at this time perhaps as far out as the Banks.

THE ICE AGE

Wherever we go on Mount Desert Island, we are reminded in some way of the great Ice Age. The cliffs, the lakes, the soil, even the plants and animals, bear witness to this period of the earth's history.

As the ice advanced from the north, it encountered few obstacles on the New England peneplane. The general southward slope and the low hills were easily traversed. The first real obstacle to be encountered in this region were the Mount Desert mountains, extending in a direction transverse to the motion of the ice. We have to imagine the mountains at this time as a maturely dissected range with an uneven crest and with deep valleys and dividing spurs on both flanks. The ice ascended the valleys of the northern flank and spilled over the crest, at first, of course, in the saddles, whence long icy tongues descended upon the southern lowlands.

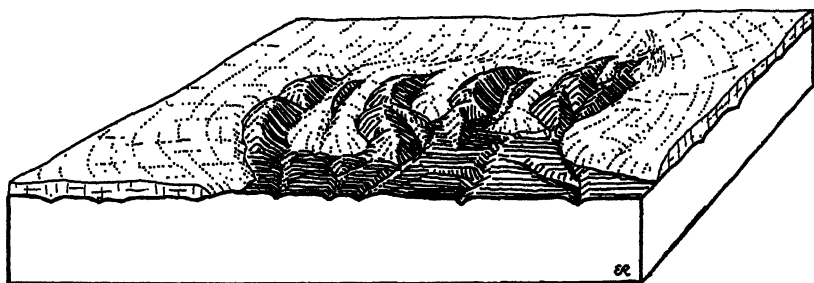


FIG. 11.—Advance of the ice through the Mt. Desert range.

For a long time the ice carved its spillways deeper and deeper into the saddles until it had cut sufficiently deep for more effective discharge, despite the increasing thickness of the ice. Such is the origin of the deep glacial troughs which give so unusual an appearance to the Mount Desert range. Only when the thickness of the ice exceeded the height of the mountains were the crests buried under a slowly moving ice sheet several thousand feet thick.

At this stage the ice movement changed its direction. This is recorded in the asymmetry of the mountains and in the form of the ice-carved ledges. In the beginning the ice was guided by the direction of the valleys, which was transverse to the main crest and coincided with the

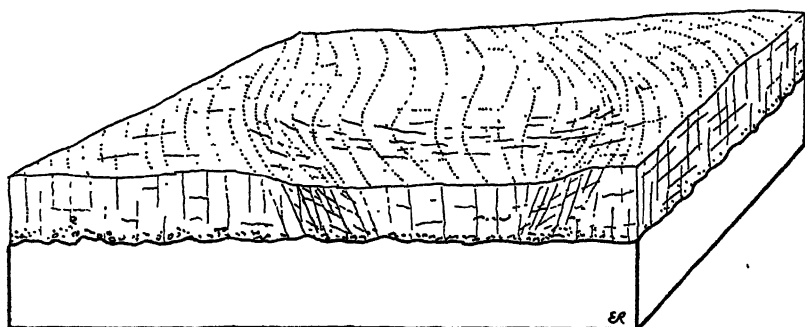


FIG. 12.—The ice over Mt. Desert. The range is completely buried by ice. At this stage the ice is supposed to have moved SE.

direction of the north-south dikes. Where the ice extended above the mountain tops, it could not be controlled further by the topography, but followed its own general direction of flow, which was more to the south-east.

During glaciation—probably due to the enormous weight of the ice—the earth's crust yielded and the region was depressed several hundred feet. As the climate became milder, the supply of ice from the north ceased, and the great thickness of ice melted gradually down. During the vanishing of the ice sheet the earth's crust, liberated from its burden, rose again. This elevation appears to have been in full swing when the ice melted away from Mount Desert Island.

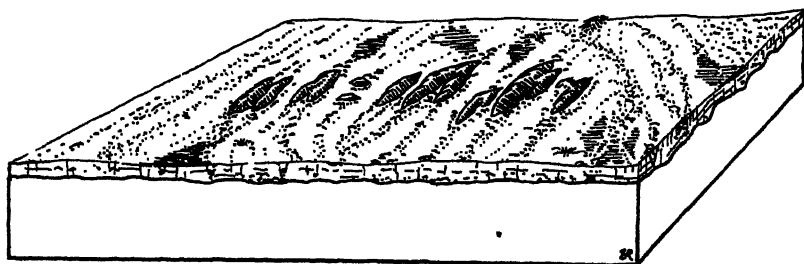


FIG. 13.—Vanishing of the ice sheet, with concentration of debris and moraines trailing from the reappearing ridges.

At this stage of the vanishing ice we have to imagine the Island somewhat similar to the present coast of Greenland. The ridges were free from ice, but in the deep valleys long ice tongues extended toward the sea from the vast frozen fields behind. The Island was still depressed and the waves of the ocean swept away the glacial debris from the out-

standing ridges. The height of this post-glacial sea is found to be about 220 feet above the present sea level, as will be shown in the next chapter.



FIG. 14.—Mt. Desert Island at the beginning of post-glacial time. Ice tongues lingering in the valleys, while the ridges are free from ice.

As the ice melted, it dropped its load. The mountains and lowlands were covered with glacial debris, and overloaded rivers started to transport and sort the material. Stream deposition of the ice-carried material may well have proceeded on a scale unparalleled at the present time.

The drainage of the Island was completely changed by glaciation. Some of the old stream channels were destroyed, and the deep glacial troughs offered new channels for the run-off. The rivers started to remove some obstructions from their courses, but that this process has not advanced very far is shown by the many lakes and swamps remaining on the Island at the present time.

Life took possession of the Island again. In the sheltered coves marine pelecipods and barnacles of an arctic type appeared. Vegetation took hold on the rocks; forest cover developed and checked the rapid stripping of the mountain sides. Fish appeared in the lakes and wild animals reached the Island and inhabited the forests. In consequence of its separation from the mainland, which was even more pronounced in earlier times than now, the flora and fauna of the Island are somewhat different from that of the mainland and still retain a more arctic character. Finally men appeared on the Island, a not negligible geological agency. Wholesale deforestation, which promoted erosion of the soil, the damming of lakes, the building of breakwaters and especially agricultural activities influenced many of the normal geological processes.

Most of the changes in their end result were very fortunate for the present inhabitants of the Island. The lofty mountains and the deep glacial troughs with their over-steepened slopes, the beautiful lakes, the

deep sheltered bays, the high-cliffed headlands invest the Island with unparalleled beauty, so that it is one of the places most highly favored by people who want to restore body and soul amid the primitive features of nature.

THE UPPER MARINE LIMIT

As mentioned in the previous section, during the vanishing of the ice the land was depressed and the sea covered the Island to a certain height. The height of this "Upper Marine Limit" is one of the outstanding problems of Mount Desert Island. The interest of the question lies not only in its bearing upon the general geological history of the region, but also in the fact that nearly all geologists who have studied the Island have expressed different opinions on the subject.

REVIEW OF THE LITERATURE

Shaler (25-p. 1027) carried the post-glacial marine limit up to 580 feet, and he thinks that the sea reached during some interglacial times above the highest peaks of the Island, over 1500 feet. His evidence is based on supposed marine cliffs and benches in the granitic mountains.

No one of the later investigators went to such an extreme. Davis (14-p. 69) thought that the marine limit exceeded 300 feet. He says: "Beds of stratified clays bearing marine fossils are found on the main land up to 200 feet." He arrives at this figure by "judging the relation of these clays to the washed gravels and sand on higher slopes." He also points out that the submerged condition could not have lasted long.

Bascom (4-pp. 124-26) places the upper marine limit at 350-400 feet. She found that the *present* rocky coast shows "(a) Sea cliffs and caves and a bench, bearing cliff debris on its outer slope; (b) Chasms bearing sand and pebble beach on their upper end; (c) Sand and clay deposits in protected places." She observed similar features at higher levels, and on this evidence she enumerates the following benches:

90-100'
165-200'
270-290'
300-340'

She also found ill-defined benches of doubtful origin at 380, 430, 480-800, and above a thousand feet.

Stone (27-p. 48) made a thorough study of the question on the adjacent mainland and nearby islands. His upper marine limit is 230 feet.

He found round (beach) gravels below the limit, and angular (glacial) gravels above. The change is rather abrupt in sheltered places on *Isle de Haut* at 220 feet.

Fairchild (17-p. 628) placed the upper marine limit at 250-260 feet. He based his conclusions on the nature of the post-glacial sediments, especially on delta deposits.

Johnson (21-pp. 135-40) doubted the marine origin of the higher cliffs of Mount Desert Island, including the Cadillac Cliffs. He does not give any figure for the upper marine limit, but recognizes the existence of marine forms at the lower levels. He characterizes the present shoreline as a young shoreline of submergence, recognizes that there was at least one submergence and one emergence during post-glacial time, and believes the actual history was one of more complicated oscillation of level.

THE CLIFFS OF MOUNT DESERT ISLAND

Many of the geologists searching for the marine limit were looking for wave-carved cliffs and benches above present sea level. There are a great many cliffs on Mount Desert Island, at every possible level. There is even some resemblance between these cliffs and the cliffs of the present shoreline. Furthermore, they are most numerous on the south-facing side of the Island, which is also the side most exposed to wave attack.

There is an essential difference between the cliffs of the present shoreline and the cliffs above. The present shoreline, with few exceptions, lies entirely in the weak rock belt, whereas the cliffs on land are mostly in the granite. In the few places where the granite is exposed to wave attack, it is a rather surprising fact that the granite does not tend to form steep cliffs, but slopes rather gently under sea level. The two types of granitic shoreline—the Baker Island type (which is entirely flat and has a boulder beach above sea level, see Fig. 31), and the Bass Harbor type (which consists of thunder holes alternating with ridges but slightly altered by wave action, see Fig. 35)—will be discussed later, but neither of them bears any similarity to the granitic cliffs in the mountains. The high cliffs of the southeastern shore do not belong strictly to the granitic shoreline because they are on the contact zone of the granite with the weak rocks.

When we examine closely the cliffs in the mountains, we find vertical walls sometimes hundreds of feet high. They do not seem to be related, however, to any particular level; in fact, if one selects at random any level, there can usually be found cliffs at that level. On such grounds almost any level can be regarded as an ancient shoreline.

The most characteristic feature of a marine cliff is the well-defined base at a persistent level. If the present shoreline were elevated, nobody could fail to recognize it by the persistency of its level; but the most striking feature of the cliffs in the mountains is their lack of persistence at a given elevation. Their bases instead of lying in a horizontal plane, are nearly always sloping.

The presence of cliffs in the mountains can be fully accounted for by regarding them as the work of the continental ice sheet. Some of the cliffs are clearly the over-steepened sides of glacial troughs. The steep cliffs of the mountain sides facing south are reasonably explained as the result of glacial plucking.

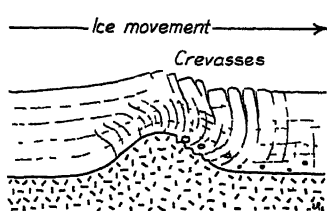


FIG. 15.—Shock and lee action of ice moving over a hill.

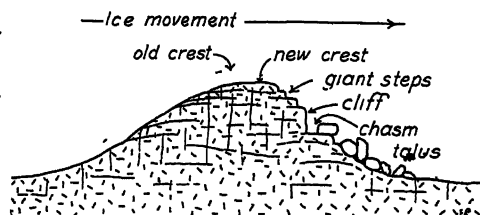


FIG. 16.—Formation of giant steps, cliffs and chasms. The stoss side will be smoothed and the crest pushed slightly forward.

GIANT STEPS

The granite of Mount Desert Island is separated into huge, regular blocks, with straight vertical and slightly curved, more or less horizontal joints. As a result of this, while a mountain may show a very smooth *roche moutonnée* form on its northern slope, on the southern slope the surface is apt to be cliffed in huge steplike terraces, for which the local name, "giant steps," is here used. The formation of giant steps is shown in Fig. 16. Because the joint planes of the granite are never exactly horizontal, the giant steps are also sloping; and this is the reason their bases are rarely horizontal—as they would be if waves had carved them.

CHASMS

There are a great many chasms in the granitic mountains, and these have been explained (4-p. 125) as significant of marine action such as has formed the chasms of the present shore. There is an important difference, however: the chasms of the present shore are perpendicular to the direction of the shoreline (Fig. 38), but in the mountains the chasms

are usually parallel to the base of the cliffs. They represent imperfectly developed giant steps, where the rock, forming the outer wall of the chasms, has not been fully removed by ice, but only moved a little distance away, as shown in Fig. 16. In other words, these chasms are widened cracks. The marine chasms are derived from removal of the rock material between two parallel joints.

There are also chasms which originated in post-glacial time. The oversteepened slopes in the granite have a very imperfect equilibrium; big masses of rock become easily parted from the parent ledge and slide downward upon the sloping joint planes by their own weight, aided perhaps by frost, snow, or the pressure of the roots of trees. The origin of these chasms is usually easily recognizable.

THE TILTED ROCK

There is a feature on the eastern slope of the Cleft which has repeatedly been referred to by the advocates of the marine origin of the cliffs (25-p. 1019, 4-p. 126). The Tilted Rock is a detached mass, separated by a chasm from the main ledge, and the uppermost stone of

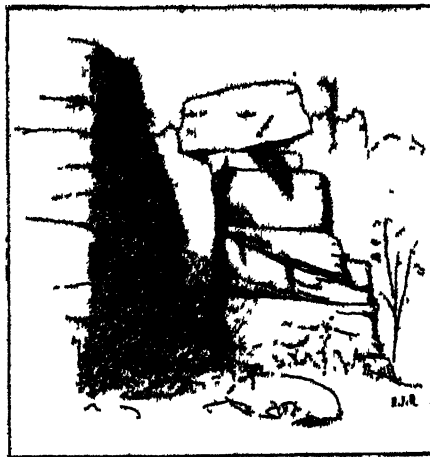


FIG. 17.—The Tilted Rock.

this mass is turned from its original position about 60 degrees. This torsion has been attributed to the action of waves. Johnson (21-p. 135) recognized the non-marine origin of this rock, and the author's examination confirmed Johnson's opinion. From the diagram, Fig. 18, it is clear that the force which turned this rock did not act from below, as a

marine origin would postulate, but from above. The most natural explanation is that snow accumulated in the triangular wedge above the rock, and its weight was more than sufficient to turn the rock around. That the force required to do this was not necessarily too formidable is

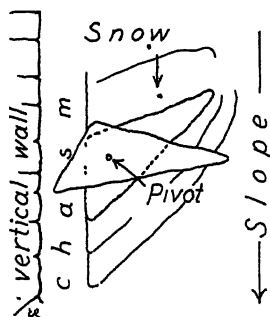


FIG. 18.—The Tilted Rock as seen from above. The diagram shows that the turning force acted from above (snow pressure) and not from below (waves).

shown by the fact that the children of Otter Creek objected to the disorderly behavior of this rock and threw it down from its pedestal. But the park officers did not want to lose one of the interesting features of the Island, and replaced the rock in its tilted position.

THE CADILLAC CAVE

Another case, cited by Shaler and Bascom as proof of former marine action, is a cave at the base of Cadillac Cliffs. Cadillac Cliffs are on the eastern slope of the Gorham Mountains and have a N-S trend. The base of the cliff starts at an elevation of 180 feet and rises to 300 feet. At an elevation of 260 feet (determined by barometer) is a cave at the base of the cliffs, in the back part of which are gravels and round boulders, lying on the floor. At first glance there seems to be some resemblance to the existing sea caves, although most of the sea caves on the present shore are formed in the weak rocks and not in the granite. The Cadillac Cliffs cannot safely be regarded as of marine origin: as Johnson (21-p. 136) pointed out, the base of the cliffs is not persistent enough in level. On the other hand, they can be fully accounted for by glacial action. This particular site seems to be the side wall of the glacier coming from the Tarn. The glacier was moving parallel with the cliffs, and it is easy to imagine that the ice loosened a wedgelike block from the nearly vertical wall and moved it slightly, leaving the rift in the rear (Fig. 19). Another possibility is that the rift may have resulted from slipping in post-glacial time. We find similar features all over the Island in every stage of development, especially along the eastern wall of Champlain (Newport) Mountain.

BEACH DEPOSITS

Johnson noted the occurrence of true elevated beaches at low levels. These are represented by sand and gravel deposits, one of which near Mr. Dorr's residence shows indistinct ridges, tentatively interpreted by



FIG. 19.—The Cadillac Cliffs.

Johnson as beach ridges. Elsewhere there are sand and gravel deposits, the nearly level upper surfaces of which may be due to wave truncation. Whatever the true origin of these obscure forms, they are all far below the upper marine limit, and give us no aid in determining that limit.

DELTA DEPOSITS

Davis and Fairchild based their upper marine limit on the height of certain delta deposits. Well assorted delta sands and gravels are found on the Island at several places, the best exposures being along Stanley Brook, where they reach an elevation of 150-200 feet.

If a clear upper limit for the delta deposits could be found, a fairly sharp upper marine limit might be determined. All the pits and quarries along the roads of the Island were carefully examined, but the result was not wholly satisfactory. Stratified sands were observed in a number of pits ranging from 80 to 500 feet in elevation; these are less well strati-

fied at the higher levels, better at the lower levels; but the transition is so gradual that no distinct limit could be found. The higher deposits do not show true delta structure; but this is equally true of some of the lower. In many cases the exposures were not sufficiently clear to make the structure evident. Even where an unequivocal deposit, like that so well exposed along Stanley Brook, permits the fixing of a marine limit, this is only the marine limit for the period when that particular deposit was laid down. It may well be appreciably below the upper marine limit. In general it may be said that the evidence available seems to carry the marine waters well up toward 200 feet, and possibly above that level; but it does not seem to fix the upper limit with precision.*

FOSSILS

Marine fossils of an Arctic type—such as *Saxicava rugosa* Lam. var. *arctica* L., *Leda arctica* Dawson (?), *Macoma calcarea* Chemnitz—were found at Birch Brook, near Seal Harbor, at an elevation of 120 feet, in blue clays overlain by stratified gravel. Similar fossils were located at Little Hunter's Brook, at an elevation of 80 feet, and at Goose Cove near sea level (7-p. 400). This signifies that the shoreline was above 120 feet in times when arctic conditions still prevailed. Certain of the stratified gravels above the blue clays are rather puzzling, and perhaps the fossiliferous clays represent not post-glacial time but some interglacial period. Altogether the evidence of fossils does not give a reliable clue to the post-glacial upper marine limit.

WASHED SURFACES

There are no cliffs sufficiently persistent in their altitude and shape to be regarded as sea cliffs. If the sea was once at a higher level, it must have been only for a very short period, and the rising of the land must have been rapid. De Geer (15 and 16) in Scandinavia found a rate of emergence of half a foot per year after the vanishing of the ice. In case the emergence of New England was similarly rapid, it is easy to understand why the waves were not able to cut benches into the Mount Desert * granite. The only thing the waves succeeded in doing was to remove the glacial till from the well-exposed places.

* Since the writing of this paper there has been published a report by Antevs entitled: *Late Quaternary Changes of Level in Maine* (2-p. 320). Antevs places the upper marine limit at 240 feet in the region of Mount Desert Island, based upon Fairchild's report and his own observations on the adjacent mainland. Antevs used mostly as evidence "wash plain" of gravel and sand at higher elevations.

There is not a trace of soil or even gravel on most exposed parts of the present shoreline. Every hilltop or ridge crest that was once an outstanding ledge confronting the full force of waves during a higher stand of the sea, likewise has little chance of retaining glacial till today. This does not apply to hillsides, because material of glacial origin could later be washed down from above the marine limit. Accordingly the hilltops and ridge crests on the eastern and southern parts of the Island were examined for the presence of glacial gravel and a sample was taken of the usually present soil. Where the soil is of glacial origin, its material may be different from the bedrock; where it derives from the weathering of the bedrock, it must show the same constituents. The soil samples were examined under a binocular microscope. If there were granite particles found on a well exposed hilltop composed of weak rocks, it seemed safe to assume that it was transported there by the ice. Weak rock particles on hilltops composed of granite were conclusive only if no weak rock inclusions or intrusions were present on those particular hilltops. The same principle applies to gravels, with the additional evidence that the gravel of glacial origin is likely to be better rounded than the gravel derived from recent disintegration of the bed rock.

Outside the lowlands (discussed later) the lowest well-exposed hilltop where glacial material was found was Flying Mountain, at an elevation of 270 feet. Although the summit of the hill is composed of a basic rock, there were a number of round granite pebbles on its top, even in the most exposed localities. The highest hilltop with distinctly residual soil devoid of foreign materials, is south of Bar Harbor, at an elevation of 220 feet. If one considers that the action of the waves would wash material higher than the actual sea level, the upper marine limit must be nearer the lower figure, around 220 feet, or even 240 feet.

The best illustration of washed surfaces is at Asticou Hill. This hill has a well-exposed crest which descends steplike to the sea. On the top, at 460 feet, there is a great abundance of glacial gravel, which continues



FIG. 20.—Profile of Asticou Hill. The minor hill (220 feet) is swept clean of glacial material.

down the slope to 200 feet. There is a minor hilltop at about 220 feet, and this is swept entirely clean of glacial material. At 80 feet the glacial gravel appears again. This latter was probably able to withstand removal by the waves because of the protection afforded by out-

lying islands and possibly also because of the presence of initially thicker glacial deposits at the lower levels. Two characteristic pictures (Figs. 21 and 23) show well the difference between the clean-swept and the debris-covered surfaces.



FIG 21.—Granite surface in the mountains above the marine limit, showing glacial material.

In studying the washed surfaces certain precautions have to be taken. I was puzzled at several places by the presence, contrary to all expectations, of little round pebbles one-half inch in diameter of different material from the bedrock on well exposed ledges at very low elevations. After a visit to the little island, the Hop, the mystery was solved. This island is the favorite gathering place for sea gulls, and the little round pebbles, chiefly of white quartz, were found in an environment which left no doubt that they were the stomach stones of the gulls.

Care must also be taken to consider only those pebbles found on the *exposed* side of the hilltop. There is usually an accumulation of gravel on the leeward sides. On the Porcupine Islands, for example, glacial deposits persist on the northern sides at present sea level.

It is interesting to note that when Stone (27-p. 48) wanted to determine the marine limit on Isle au Haut he looked for round pebbles *below* the marine limit. The author looked for round pebbles *above*

the marine limit. Stone compared beach gravel with the less rounded glacial gravel in the *sheltered* places, while the author compared glacial gravel with the still more angular residual gravel of weathering on the *exposed* places. The method of Stone was not adaptable to Mount Desert



FIG. 22.—Granitic surface swept clean at lower levels, below the marine limit.

Island because most of the sheltered valleys are covered with deep soil and forests.

Although the evidence of the wave-washed cliffs is fairly clear in placing the upper marine limit at or a little above 220 feet, there are two forms of evidence which might seem to contradict this figure. First, fluvio-glacial deposits are found in the valleys down to 80 feet. Their nature and position do not admit any other interpretation than that they were formed on dry land by melting waters from the ice. This would mean that at the time of melting the Island was dry at least down to the 80 foot level. The two figures can be brought into accord if we assume that ice tongues lingered long in the valleys when the ridges were free of ice. Similar conditions now prevail in Greenland. The melting of the ice tongues at the time when the Island had arisen produced the fluvio-glacial deposits now found at lower levels than the upper marine limit. A re-advance of the ice would produce a similar effect, but there is no other evidence that this has occurred.

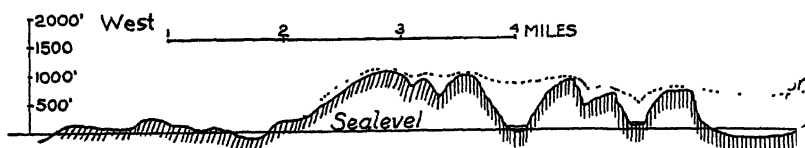


FIG. 23.—Generalized profile of

The other apparently contradictory evidence is the abundance of glacial gravel on the lowland, even on such well exposed places as, for example, the Cranberry Islands. Here we may assume that the big waves were broken on the shelving sea bottom before they reached the shore, and that the smaller waves were not able to remove the greater amount of glacial material characteristically found on the lowland areas. Only the thinly buried, well exposed hilltops adjacent to steep slopes could be swept clean of debris during the short time the rapidly rising land was exposed to wave action.

FEATURES DUE TO GLACIAL EROSION

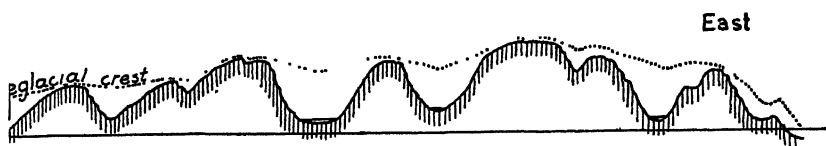
A number of features due directly or indirectly to glacial erosion, such as *roches moutonnées*, plucked cliffs, giant steps and chasms, are discussed in a previous section; so also are some special features, such as the Tilted Rock and the Cadillac Cliffs, because of their direct bearing upon the question of the upper marine limit.

THE GLACIAL TROUGHS

The most peculiar features of the Mount Desert Mountains are the long narrow notches across the range, giving the impression that the mountains are composed of N-S trending structural ridges.

Closer examination shows that the ridges are not of structural origin, but are erosion features in a homogeneous granitic mass. The typical U-shaped form of the deep notches leaves us in no doubt about the nature of the agency which performed this erosion. These notches are typical glacial troughs, as was recognized by Shaler (25-p. 1008).

Glacial troughs are common features of *local* glaciation, frequently radiating out from the center of a high mountain mass. The glacial troughs of Mount Desert are strictly parallel, and have no relation to any possible local center of ice accumulation. The continental ice sheet did not commonly form troughs, but under special conditions it did so. The conditions responsible for the formation of troughs on the Island may be summarized as follows:—



Mount Desert Island

As the continental ice sheet advanced from the north, it encountered an obstacle in the form of an elongated mountain mass with crest transverse to the ice movement. The mountain mass was at this time in the mature stage of development, with deep-cut valleys and an uneven crest. The valleys trended in a general N-S direction, transverse to the crest, but parallel to the direction of main joints and dikes. As the ice advanced from the north, it utilized the N-S valleys, spilling across the crest of the range in saddles on the divide, and deepening valleys and saddles into glacial troughs.

The most apparent thing in these troughs is their regular arrangement. There are eight deep troughs in a stretch of twelve miles, one to about every one and a half miles. It is not probable that the saddles on the pre-glacial mountain crest were placed so evenly. Initial notches developed probably in each saddle, but only those notches were able to develop fully which had a sufficient supply of ice. Where the saddles were too close to each other, the more advantageously placed ones were able to discharge most of the ice and only imperfect notches developed in the less favorable places. There are about six to eight imperfect troughs or notches on the Island, representing every stage of development.

THE LAKES

Where the ice passed through the narrow troughs, its rate of motion was more rapid than elsewhere. This meant increased erosion power at the narrowest places just as streams and currents deepen their channels in narrows. As the ice vanished from the deep places, lakes were left behind. The lakes, enclosed in the narrow parts of the valleys, are the most attractive features of the Island.

During the vanishing of the ice the troughs were filled with ice tongues for a long time, and glacial debris was deposited at their southern ends. This material helped to fill the lake basins at the south, and pushed the lakes rather toward the northern part of the troughs. Artificial dams also help to keep them at their present level, but their original basins are carved directly in the bedrock.

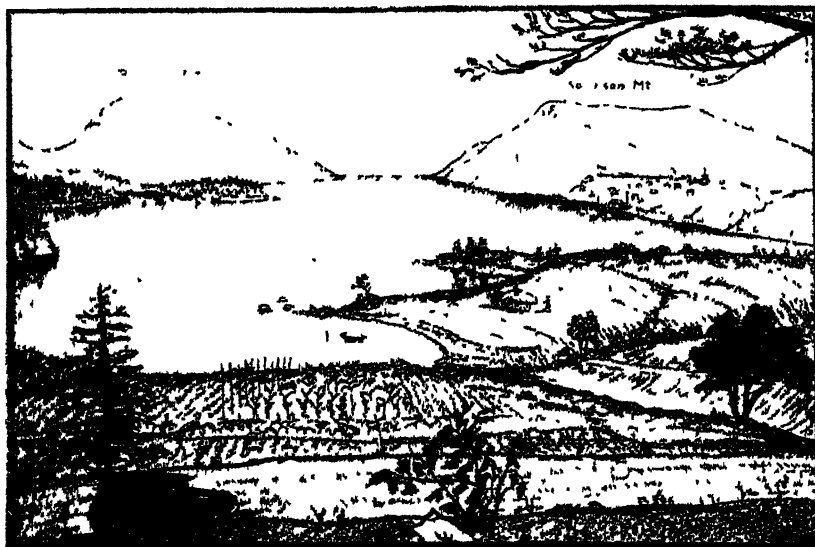


FIG. 24.—Somes Sound looking south. An example of a submerged glacial trough, or fjord. Excepting the Hudson River gorge, Somes Sound is the only fjord of the eastern United States.

In one instance (Somes Sound) this over-deepening went so far down that the trough is at the present time submerged under sea level. Submerged glacial troughs are termed *fjords*. The word "submergence" does not necessarily imply actual change in the sea level. It is well known that ice streams are able to cut their channels below sea level, and that when the ice vanishes, the sea may enter the abandoned glacial channels without any change in sea level.

Somes Sound is the only true fjord (although a poorly developed one) besides the Hudson River Gorge in the eastern United States (21-p. 103). The entrance to Somes Sound is 41 feet, the middle part of it 153 feet deep. If the land should emerge about 50 feet, Somes Sound would be transformed into a lake like those occupying the other troughs.

THE ASYMMETRY OF THE MOUNTAINS

One of the most noticeable features of the ridges is that they have a smooth, western slope and a cliffed, eastern slope. This asymmetry is prevalent all over the Island, but is most characteristic in the western part, and slight in the southeastern granitic hills (see the mountain on the left side of Fig. 24).

Asymmetry of ridges may be due to several causes, including geological structure, differences in frost action, in local glacial erosion, in insulation or in amount of vegetation, as well as to the deflective influence of the earth's rotation. On the Mount Desert range the rocks are of homogeneous granite, with no such joint structure as could produce the asymmetry noted. The effect of the earth's rotation would in many cases be the reverse of that observed. There is no great difference in frost action, insulation or vegetation on opposite slopes. As the most plausible explanation of the asymmetry we may assume the action of the ice in smoothing stoss and plucking lee slopes.

If we examine the smooth and cliffed ledges of the mountains, we find that the cliffing is not on the southern side, as one would expect if all the ice moved from north to south like that in the restricted troughs, but on the southeastern side. Certain deep glacial grooves on the mountains gave also a southeasterly direction. Where the granite is freshly uncovered, it shows a finely polished surface with well preserved striations. Unfortunately the striations are weathered off from the barren mountain tops, where only the polished surface is preserved on some of the harder quartz grains.

The direction of the glacial striations was measured at many points and a map (Fig. 25) compiled which includes results of previous measurements by Shaler (25-map). The map shows—aside from smaller irregularities—that the general directions of ice movement at the time the glacial striations were made was not the southeasterly direction of the *roches moutonnées* and grooves, but the nearly N-S direction of the glacial troughs. The *roches moutonnées* and grooves on the tops of the mountains show the direction of movement when the ice passed freely over the mountain tops. Presumably the glacial striations show the direction of movement in the last stages of glaciation.

As long as the ice was thin at the beginning of glaciation the direction of its movement was guided by the pre-glacial, nearly N-S valleys, in the place of which deep glacial troughs were carved. When the ice grew thicker and extended above the mountain tops, the direction of movement changed from a nearly N-S to a NW-SE direction. This ice movement smoothed the ascending slopes and cliffed the descending sides, thereby making the western walls of the already established N-S glacial troughs steeper than the eastern walls.

These differences in local directions do not necessarily imply an actual change in the general direction of the ice movement. It is conceivable that the general direction of ice advance during all this period was to the

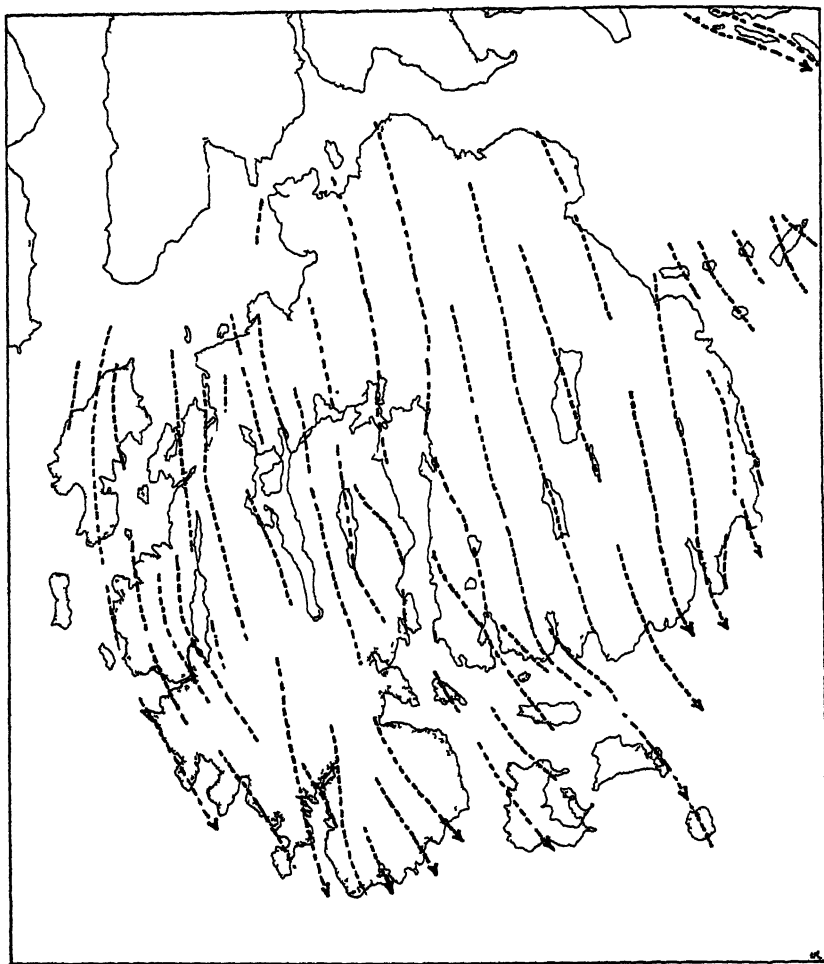


FIG. 25.—Trend of the glacial striations on Mt. Desert Island.

southeast, but that when the ice was thin, it was more influenced by the N-S trending topography. Since in the bottoms of the glacial troughs the ice had to move in the direction of the channels at all times, there must have been during maximum glaciation a twist in the ice, a south-east direction in the upper mass of ice and a nearly N-S direction in the bottoms of the troughs. As the bottom ice left the glacial troughs at their southern outlet, it maintained its N-S direction for a while, and this explains the absence of asymmetry in the southern granitic hills.

The higher members of these hills, as Day Mountain, are just as asymmetrical as the northern mountains.

It is noteworthy, however, that the glacial striations do not show the NW-SE direction in the northern part of the Island, which was scratched before the ice entered the mountains. This may be interpreted as an actual change in the direction of the ice movement to a nearly N-S direction during the later stages of glaciation.

THE TREND OF THE TOPOGRAPHY

The ice tends to deepen and straighten the valleys which conform with its direction more than the valleys across it, and it develops a trend of the topography which can be mistaken for the structural trend. The glacial and structural trends are often superimposed one upon the other; sometimes one is stronger; sometimes the other; and sometimes, if they are equal in strength but at right angles as to direction, the topography develops a peculiar checker-board effect.

On Mount Desert Island, in the granitic mountains the structural and glacial trends coincide, but in parts of the weak rock belt the structural trend is locally transverse to the ice direction and a real checker-board topography is formed. This feature is especially marked in the southwestern part of the Island. The topographic map shows it clearly. In other parts of the Island the glacial trend is the prevailing one. The tendency of the ice to flow around the two sides of the mountain is well expressed in the topography. Note the southwest trend of the region around Bartlett Island, changing to south at Seal Cove.

THE QUESTION OF LOCAL GLACIATION

The most characteristic features of *local* glaciation are cirques, the semi-circular hollows excavated by the headward erosion of local glaciers. North of Upper Hadlock Pond on Sargent Mountain we find two hollows which suggest this origin. Both are very crude in form and far from being typical cirques, but we should recognize the possibility that cirques were actually formed in this region.

It was probably a very long time after the climate turned cold in the beginning of the Ice Age before the continental ice sheet arrived on Mount Desert. During this time the climate of Maine may well have been colder than that of Alaska today, where even lower mountains than Sargent Mountain have glaciers.

It seems less probable that cirques originated at the time of the vanishing of the ice sheet. The cirque form appears to have been par-

tially destroyed by later ice invasion, and the half of the northwestern cirque is cut through by a glacial notch. From the studies of De Geer, Antevs and others we judge that the vanishing of the ice sheet was a rather rapid process. The ice front retreated from a hundred to a thousand feet in a year, indicating that the climate became rapidly warmer and that it was already warm while there was still ice present.



FIG 26—Cirques in the Sargent Mountain group.

Sargent Mountains constitute the central big group of mountains on the Island, and the most favorable place to observe cirque development. It is peculiar that no cirques are present on their northern flank. We may perhaps assume strong north winds throughout the year when the continental ice sheet was not far away. Similar strong winds are blowing outward from the continental ice sheet of Greenland, and from the Antarctic. Such a wind would blow the snow from the northern flank over the crest, and permit large masses of snow to accumulate in hollows on the southern slopes. Furthermore, daily alternation of melting and freezing may be stronger on the southern flank than on the northern, and this process is favorable for glacial plucking and for cirque carving. Thus in certain cases mountains may have better cirques on their southern exposures than on their northern. If short glaciers descended from cirques

on Sargent Mountain, their traces could not in any case be separated from those of the later continental ice.

No other indications of cirques were observed.

THE QUESTION OF MULTIPLE GLACIATION

In the central part of our continent, where deposition is the main process of glaciation, several glacial periods can be distinguished, separated by warm interglacial periods. The sequence of the glacial periods is not so clear in the northeast, where erosion was the dominating process and the terminal moraines are often under the sea.

The best evidence for a break in glaciation is a succession of deposits in which one member has its upper surface leached, oxidized, and perhaps eroded or covered with peat and fossils, while the next higher member consists of unaltered glacial till.

There are on Mount Desert Island a great many sand pits where the glacial beds are exposed down to bedrock. The author examined these pits with this problem of multiple glaciation in mind, but in none of them did he find any significant break in the deposition. Perhaps deeper deposits at the bottoms of certain basins would give better evidence. Unfortunately there are no satisfactory well records available on the Island. Nowhere on the Island did the author find the slightest trace of pre-glacial soil, not even in depressions and rock crevices.

Bastin (5-p. 12), investigating the neighboring districts, sought evidence of multiple glaciation in glacial striations crossing each other on the bedrock. Cross striations are rather rare on Mount Desert Island. Some were observed at Robin's Point, where they seem to be of very local occurrence. They can be explained satisfactorily as due to local and temporary variations in ice movement. As glacial striations are usually very delicate features and a new period of glaciation would be likely to destroy them, cross striations due to multiple glaciation should be of relatively rare occurrence.

THE POTHOLES

On the southern flank of Cadillac (Green) Mountain there are a number of round holes in the granite, two to ten inches in diameter and somewhat less in depth, known as "The Potholes." The usual explanation is that boulders were rolled around by water from the melting ice and excavated holes in the bedrock, as is often done in present stream beds.

These pot holes are much more common features of the granite than is generally thought; they were found practically everywhere in the granitic mountains in all stages of development, but usually not apparent because they are filled with soil. They are most common on the southern flank of the mountains. Apparently they have no necessary relation to the immediate local relief. They are most frequently found in flat places, but are also present on slopes.

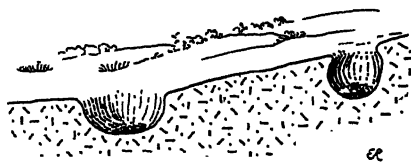


FIG. 27.—Potholes in granite.

Once by hammering at the bottom of a small pothole a piece of green epidote was recovered. Upon repeating this, in most cases the epidote was found in the smaller potholes, although this did not hold true for the larger holes.

The occurrence of epidote offers a possible clue to the origin of the potholes. Little clusters of green epidote are found scattered through the granite in many places. These weather out very readily, leaving small round holes an inch or two in diameter. Such holes are abundant in the granite and are quite commonly filled with water. Alternate melting and freezing of the water, together with chemical corrosion, has widened and deepened some of these holes, while running water, swirling sand and gravel in them, perfected their form and enlarged them. In the locality specially known as "The Potholes" there is the favorable combination of considerable amounts of water at certain seasons and much epidote scattered through the granite. That the potholes are more common on the southern flank may be explained by the more frequent alternation of freezing and melting there, while complete removal of the epidote from the greatly enlarged cavities is to be expected.

THE SADDLE PONDS

The glacial troughs are separated by long narrow N-S ridges. There are local saddles in the crests of these ridges, and in the middle of such a saddle there is frequently a pond. Among the most characteristic ponds of this kind are Saddle Pond on Cadillac (Green) Mountain, one north of Gorham Mountain, another south of Kebo Mountain. Where there is no pond, there is usually a marshy basin in the middle of the

saddle. The rocks in the saddles show smooth western flanks and cliffed eastern edges, as if the ice direction had not been N-S but W-E or NW-SE. This explains the presence of the saddle ponds as minute glacial trough lakes formed under the same conditions as their big sisters in the bottom of the big N-S glacial troughs. In the saddles the ice moved from west to east because, as the ice attained its most easterly direction during the height of glaciation, it used the saddles as spillways, passing from one glacial trough to another. This W-E-moving ice transformed the initial saddles into small glacial troughs, and over-deepened these in places just as it did the big N-S glacial troughs.

GLACIAL AND OTHER DEPOSITS

THE GLACIAL DEPOSITS OF MOUNT DESERT ISLAND

The glacial deposits of Mount Desert Island can be classified into three types:—

1. Fluvio-glacial deposits
2. Delta deposits
3. Unstratified till

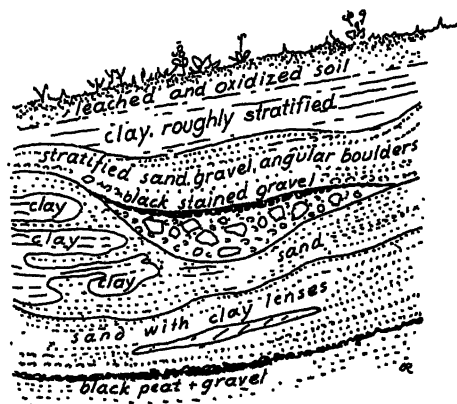


FIG. 28.—Fluvio-glacial deposits at Whales Back.

FLUVIO-GLACIAL DEPOSITS

This is the most common surface material over the Island. Its most characteristic features are a rough stratification with violent variation in size of material and dip of beds, and excessive cross-bedding, often with very steep angles. Material of this type can be found between eleva-

tions of 80 and 500 feet. At the higher levels the cross-bedding and the variation in dip are more pronounced, at the lower levels the strata become more evenly bedded and form transition to the delta deposits. The character of the material indicates deposition by melting waters running down the slopes, excessively overloaded and varying constantly their volume and velocity.

The material varies from the finest clay to big boulders and represents the entire lithology of the country to the north. A small amount of the gravel represents material brought to the Island from a distance. Fossiliferous limestones are occasionally found, probably derived from the Silurian rocks about one hundred miles to the north. The major part of the material does not seem to have been transported more than a few miles. In the northern part of the granitic belt weak rock gravels are in excess, but in the southern part of the granitic area the weak rock gravels are much less abundant than those of granite. It seems that the ice—at least the lower part of it which carried most of the drift—hardly moved at all. Naturally the most violent variation of materials is on slopes high up in the mountains; during transportation the material underwent sorting; therefore we find the rougher stratification of the higher slopes becoming more regular and more horizontal nearer sea level.

THE DELTA DEPOSITS

In several places on the Island, especially in sheltered valleys, we find exposures of finely laminated and well sorted sands forming strictly parallel laminae inclined 20° — 25° . This series of beds is sometimes truncated by a less perfectly stratified horizontal series, often containing much coarse gravel and even cobblestones. Such type of deposition is characteristic of delta deposits. As a river bearing glacial debris from the melting ice entered the sea, the current was checked and it dropped its load to build a gradually expanding delta. The angle at which the material came to rest on the front of the delta was the angle of natural repose, under sea water about 25° ; successive additions to the delta front formed the "foreset" beds. As the load and velocity of the rivers varied, the laminae became finer or coarser, while still coarser material was left stranded on the delta surface to form the horizontal "topset" beds.

Complications arose through the gradual emergence of the land. The delta deposits, which were formed a few feet below low tide level, became exposed to the force of the waves. Only in sheltered bays were

they able to survive and emerge above sea level. With this emergence the delta moved seaward and new delta deposits were laid down on top of the outer beds of the old delta.

THE UNSTRATIFIED TILL

It is especially in the bottoms of the deeper valleys that we find unstratified till, composed of debris of all sizes, ranging from clay to big boulders. These deposits are well exposed in the open coves of the south shore, where they are cut back by the waves. Their thickness is considerable, up to 30 feet or more. Probably enough debris was removed from hill-sides and valley bottoms and dragged along the bottom of the ice to form the ground moraine represented by these deposits, which are unstratified because dropped by the melting ice without the sorting action of water.

OTHER DEPOSITS

THE BLUE CLAY

In some localities, as in the smaller brooks on the south shore, a fossiliferous blue clay is found. This clay is extremely fine and plastic, blue in color, with streaks of black organic matter locally present. It is so soft that I was able to push into it by hand a pipe nine feet long. The material seems to be quite homogeneous, showing no variation in color or texture.

The blue clay evidently represents deposition in very quiet water where no disturbances took place. Well preserved barnacles indicate that it could not have been very far from the shoreline. The clay is found usually in the shorter valleys, such as Birch Brook, east of Seal Harbor and Little Hunter's Brook. It is covered with stratified gravels, some of which are very evenly graded, as at Sargent Brook, while others are similar to the fluvio-glacial deposits, as in Birch Brook. The height of the blue clay ranges from 80 to 120 feet above sea level.

The fossil content of the blue clay shows that the sea stood at the time of its deposition more than 120 feet above the present level, and that there were subarctic conditions at that time. Clay in such purity indicates that at the time of deposition no glacial debris was being actively deposited in the vicinity.

THE SURFACE DRIFT

Over the entire Island the uppermost layer of stratified deposits differs from the lower part. Usually it is devoid of stratification; it is more brownish in color and generally of a coarser material than the deposits

below. The transition to the stratified drift is rather abrupt, and is usually marked by a fine layer of clay. The uppermost few inches consist of gravel and boulders, with black soil. On examination with the microscope the unstratified superficial material and the stratified material seem to be much alike; the only difference is that the sand grains of the surface drift are coated with a very fine layer of clay, while the stratified sand is relatively clean. After washing, the two materials appear almost identical. Closer observation of sand pits disclosed that there is often in the superficial drift a vestige of stratification; and the fine clay layer which usually separates the two kinds of material is not persistent—the dividing line jumps from one fine clay layer to another.

The foregoing facts are interpreted to mean that the superficial unstratified drift is an alteration product of the stratified drift. Surface creep and other movements in the superficial zone have largely destroyed the stratification and mixed the thin clay layers with the sand. Leaching of this surface zone ceases where the descending waters encountered an undisturbed clay seam and were by it deflected laterally.



FIG. 29.—Residual soil on Robins Hill.

POST-GLACIAL SOIL OF WEATHERING

Robins Hill is composed of black granite (diorite), which decomposes readily. The granite boulders shown in Fig. 29 are in place, or but slightly moved. The soil between these boulders is a granular mass of angular fragments from the minerals which composed the black granite, and the thickness amounts to several feet. As mentioned

above, all the granitic mountains and hills have a forest covering except the tops of the ridges. This forest grows in a scanty soil, most of which is not glacial soil as might be expected, but residual soil due to weathering.

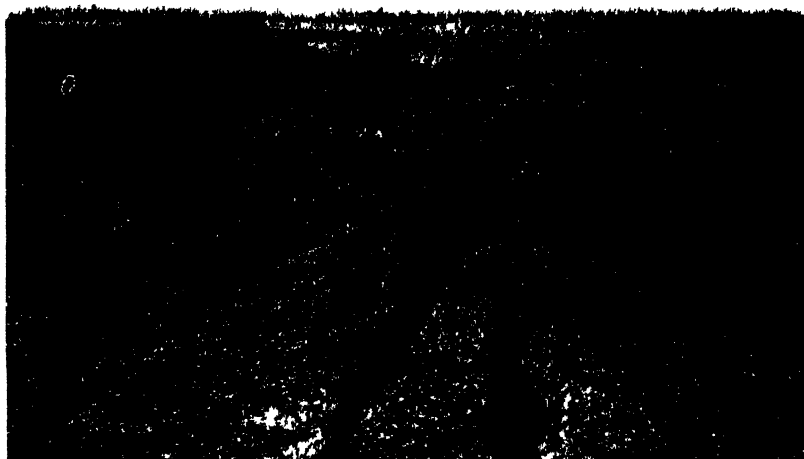


FIG. 30.—Cracks in the granite enlarged by weathering.

The formations of the weak rock belt weather still more readily. The rocks on the surface disintegrate into angular boulders, and the cracks between them become filled with a reddish soil.

TALUS SLOPES

After the vanishing of the ice, the over-steepened walls of the glacial troughs could not long stand in their unstable position, and much of their material tumbled down, forming talus slopes composed of big boulders. Some of these blocks are of great size, as the Giant and Bridge on the southern slope of Jordan Mountain. Another good talus of large blocks is found above the bridge path on the Rockefeller estate on Bar Hill. Many of the rocks show glacial striations on one side, proving their post-glacial origin.

ERRATICS

All over the Island there are big boulders of foreign material, strangers to these mountains. These *erratics* or ice-carried boulders sometimes

are of enormous size; one on the estate of Professor Luquer on Sols Cliff measures about twenty feet in greatest diameter, and forms a giant monument of the icy past.

SHORELINE DEVELOPMENT

SHORELINE OF SUBMERGENCE

The shoreline of the Island belongs to the class of shorelines of submergence. This term does not imply that submergence was the *only* movement nor even that it was the *latest* movement; it means only that the forms of a dissected land dominate at the shoreline and not the forms of a smooth sea bottom. Investigations of the sequence of changes in the past are discussed in a previous section. In the following paragraphs the features of the *present* shoreline are discussed.

The shoreline of the Island may be subdivided into three types: one developed on granite; another on weak rock; and a third on the contact zone between the two types of rock. All three situations show different shore forms, depending on the initial character of the shore (steep or flat), the direction of dominant wave attack, and amount of glacial till or other blanketing deposits.

THE SHORELINE ON GRANITE

Most of the shoreline of the Island is within the weak rock belt. There are only two places where the shoreline is on granite, but both show very interesting features.

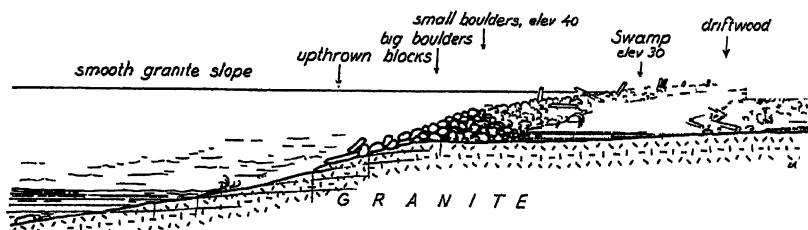


FIG. 31.—The Baker Island type of shoreline. This shoreline consists of a relatively gentle slope of granite crowned by a dam formed of uphurled boulders. Back of this dam the inland waters are ponded.

(a) *The Baker Island Type of Shoreline.*—The most peculiar shoreline is developed on Baker Island, a round little island about one mile across, south of Mount Desert, where it is fully exposed to the Atlantic waves. At this place, where we might expect to have the highest cliffs, we find a smooth, gently sloping rocky platform, which allows the waves

to ascend high up the shore. Here the force of the waves is broken by a dam of giant blocks of granite, reaching about forty feet above sea level. This boulder dam ponds the inland waters of the island and a string of swamps is formed behind it.



FIG. 32.—The southern shore of Baker Island. Note the gentle seaward slope of granite, and the heaped-up boulders above.

Bascom and Johnson attribute the development of the smooth slope of granite primarily to the direction of the joint planes, which here dip at a low angle toward the ocean. Such a smooth sloping shore is very characteristic of many outlying islands composed of granite. These slopes occur not only on the most exposed side, but on three sides or even all around the islands, as shown in Fig. 33. This would imply that the joint



FIG. 33.—Small granitic island in Penobscot Bay. Islands like this have smooth, gently sloping, rocky shore on all sides and no cliffs, probably the result of exfoliation.

planes dip everywhere slightly towards the sea, and hence that the direction of jointing must change on each side of the island.

This was at first thought to be incredible, and the assumption was made that the granite has hidden joint planes in nearly every direction, the waves working along those planes which suit best their profile of level. Professor Johnson called the author's attention to the fact that the change of dip of the joint planes so as to give seaward-sloping fractures all about an island is not only credible but a phenomenon to be expected where hills are partly submerged.

When granite which crystallized under very great pressure reaches the surface through erosion of overlying beds, the compression is released and tension cracks develop which are roughly parallel with the surface, as has been described for the exfoliation domes of the High Sierras. Scaling-off along this crack may be the main cause of exfoliation. It seems possible that all of the curved subhorizontal joint planes on the island are of this origin. As they developed parallel to the surfaces of the rounded hills, they slope everywhere toward the sea, thereby producing smooth, gently sloping shores.



FIG. 34.—Exfoliation fractures on a partially submerged granitic hill.

The small vertical cliffs developed by cross fractures passing from one exfoliation plane to the next are favorable points of attack for the waves, and huge blocks of granite are rifted loose and hurled up on the shore. The sizes of the upturned blocks are sometimes astonishing. Blocks from 10 to 20 feet long, and 2 or 3 feet thick, lifted by the waves, are not uncommon. The boulders of larger size are at the base of the natural dam or beach ridge, and the size decreases near the top and on the landward slope; there the boulders are about the size of a man's head and well rounded. It is surprising that this dam is developed also on the north-facing corner of Baker Island, where the waves have only a few miles' fetch. The extraordinary power of the northerly waves will be referred to later.

It is worthy of note that similar boulder dams were not found inland at higher elevations. Probably the sea never stood for any considerable time at any higher level in post-glacial time.

The Baker Island shoreline illustrates the features that occur where strong waves attack initially low land of granite.

(b) *The Thunder Hole Type of Shoreline.*—Where the waves attack vertically jointed granite with an originally steep surface slope, the result is a shoreline which might be called a *Thunder Hole* shoreline, after the chasm of this name on Mount Desert.

The granite is usually parted by joint planes into large rectangular blocks. The vertical planes are several feet apart and are very persistent in direction. The nearly horizontal joint planes, described above, are close together, but inclined slightly in varying directions and are usually curved. Because of the large size of the granite blocks, small waves leave them practically unaffected, and only the biggest storm waves are able to attack them effectively. If the original slope is steep, even storm waves are unable to hurl up blocks as on the Baker Island type of shoreline. The strong waves remove blocks along the parallel, well developed vertical joints, especially along the S-SE set of master joints, which on the southern shore is nearly perpendicular to the shoreline. The separated blocks are carried downward on the submarine slope and in place of the block a hole is left into which the water is crowded during a storm and has no other escape than upwards. These upward-forced waves have a tremendous impact, rift up further blocks at the base of the hole, and finally develop a chasm with straight vertical side walls called Thunder Holes.

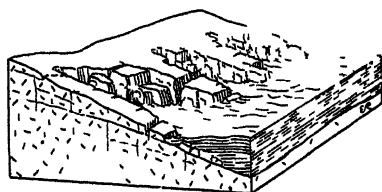


FIG. 35.—A Thunder Hole shoreline consists of a series of marine chasms separated by ridges, the seaward ends of which are but slightly cliffed.

It is a wonderful sight to stand above the rocky slopes and watch these deep chasms into which, at every swell, the waters roar with a voice like thunder. Because of this impressive view, the granitic type of shoreline looks extremely rugged and cliffed. But when we look upon the profile sideways from a distance, and do not see the thunder holes—only the profile of the ridges between them—we note that on this profile very slight cliffing is discernible. It is surprising to find glacial striations on these spurs nearly down to sea level.

When the granitic shoreline is not exposed to full-sized waves, there is hardly any noticeable effect. The glacial till is stripped off, but the rocks show glacial striations, the waterline is marked by a strip of barnacles, and the rocks pass unaffected below sea level.

THE WEAK ROCK SHORELINE

The effect of waves on the weak rocks is very different. Although the weak rocks are composed of a great variety of formations, their behavior under wave attack is rather uniform. They all have one property in common: the rocks have an intricate network of joints, and the small fragments break off easily.

On this much-jointed mass even the effect of small waves is noticeable. The retreat of the shoreline is much more rapid than that bordering the granite. The wearing back of the entire mass results in a rather straight vertical cliff, the height of which depends upon the steepness of the original slope. When the shore is sufficiently high, there may be a notch or sea cave at sea level, and a straight, sometimes overhanging cliff above. The cliffs reach to a height such as is found nowhere else along the Atlantic coast of the United States.

It is rather surprising that on the northern shore of the Island, where the waves have a fetch of only a few miles, we find some of the highest cliffs, arches and sea caves.

The assumption that the sea once stood for a considerable time at a higher level to form the upper part of the cliffs is not probable. The rate of the emergence seems to have been relatively rapid, as is shown elsewhere in this report. It is tentatively suggested that following the glacial time, the northwest blizzards were much more violent than at the present time. The great anti-cyclone formed over the ice cap at the time when the ice was somewhat north of our latitude must have produced northwest blizzards of unparalleled fury.

THE SHORELINE OF THE CONTACT ZONE

Nowhere on the Island is the difference in behavior of the granite and weak rock under wave attack better exhibited than along the southeastern shore formed along the contact between these two types of rocks. As the molten granitic mass forced its way into the older rocks, it penetrated along fractures and eventually incorporated and partially fused large masses of the older series. This irregular contact zone of the granite and weak rock formations is usually several hundred feet wide.

The original landform against which the sea came to rest was an indented surface, consisting of spurs with glacial troughs between them perpendicular to the shoreline. The slopes at the southern ends of the spurs were initially steep and cliffed. As the sea attacked these cliffs, it found the confused mass of the contact zone. At first it worked against the outer portions, in which the weak rocks predominated. In these



FIG. 36.—Great Head, one of the highest headlands of the eastern United States.

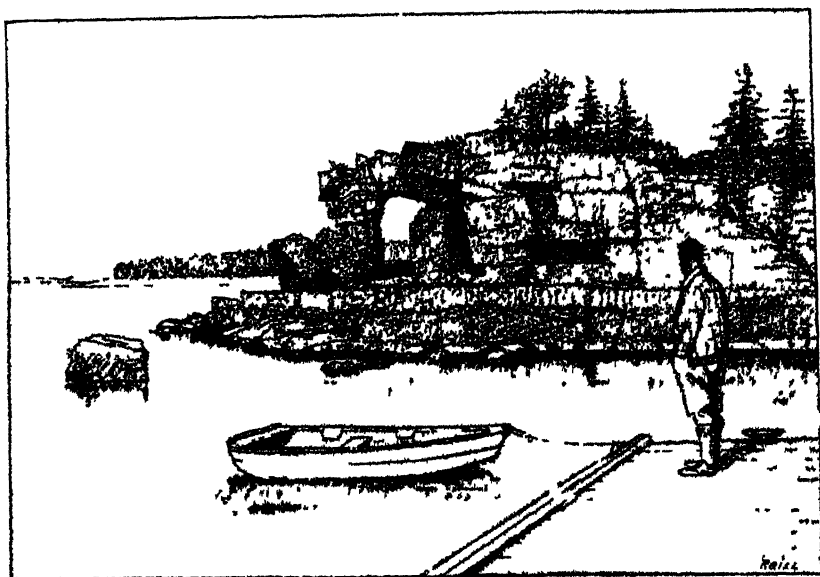


FIG. 37 —A marine arch near Salisbury Cove

weak rocks high marine cliffs developed; as the cliffs receded, they penetrated more and more into the granite. The present cliffs are at the place where the predominating rock is granite, but the unusual height of the cliffs is inherited from the weak rock belt.

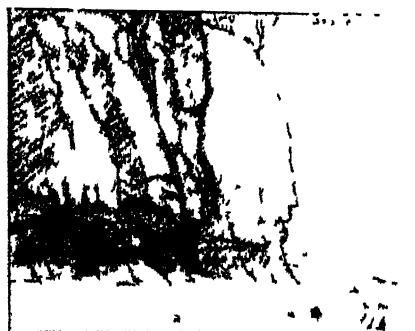


FIG. 38 —The Ovens. Marine caves and arches in weak rocks on the northern shore

Some minor examples illustrate the different behavior of the granite and the weak rocks under wave attack. Figure 39 shows a portion of the shoreline east of Sandy Beach (Newport Cove). The outer shoreline is developed on steep slopes of granite, but the waves have cut through

its contact zone in one place and carved a sea cave into the weak rock series (locally a part of the granite is here south of a mass of the weak rocks), the cliffs overhanging above. The form of the small rock mass in the foreground of Fig. 39 is noteworthy. It is composed of granite on

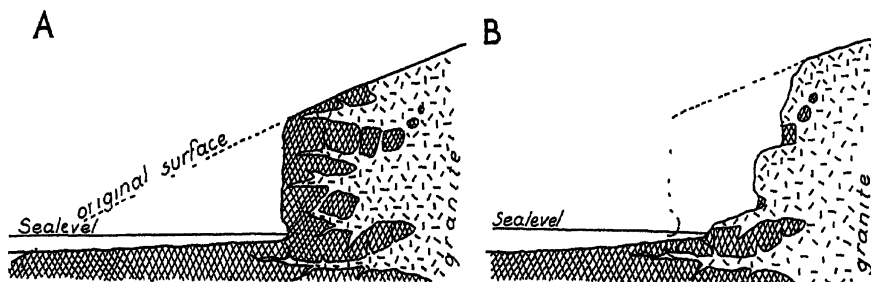


FIG. 39—Inherited cliffs of the contact zone shoreline.

the seaward side and of weak rock on the landward side. The granitic side, although fully exposed to the waves, is little affected, but the weak rock portion—although it is on the protected side and gets only the rebound waves—shows sharp cliffing. Hundreds of cases illustrate similar behavior of these contrasted rock types.

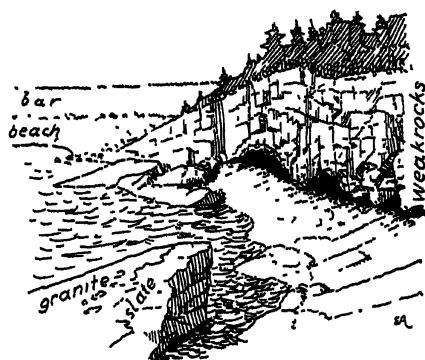


FIG. 40—Caves near Sandy Beach (Newport Cove) in cliffed weak rocks near granite contact.

(a) *The Coves.*—The physiographic significance of the coves is in their bearing on the problem of post-glacial submergence. If the land once stood higher during post-glacial time, streams may have cut post-glacial notches in the bottoms of the ice-carved valleys. If the land was later submerged, the valleys would be transformed into coves, and the post-glacial notches—if undisturbed—would pass under sea level.

Figure 41 shows the different types of coves which would have developed by 1) a submerged river valley; 2) an ice-carved valley partly occupied by the sea without post-glacial emergence or development of a notch; 3) submerged glacial valley in which a post-glacial notch was cut when the land stood higher. The two latter cases may be modified

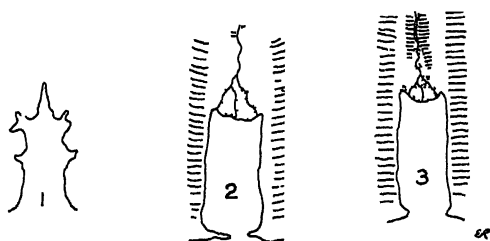


FIG. 41.—The form of coves: 1) submerged river valley; 2) glaciated valley now partially occupied by sea; 3) glacial valley with a post-glacial notch, indicating former higher stand of the land.

by stream deposition. Only deep sheltered coves can be taken into account, because open coves are subject to modification by wave attack. Of course, slight incisions made by streams due to tidal variations or to seasonal changes of stream volume and channel size should not be mistaken for post-glacial notches.

In most of the deep coves, especially in Otter Creek Bay, the incision of the stream flowing into the cove is much deeper than the tidal range or seasonal changes in streams would account for. Apparently we find in this fact support for the view that sometime in the post-glacial period the land stood higher than at the present time, and that the last movement was a slight submergence. The drowned river pattern at the northern end of Somes Sound and at Marshall Brook also support this view, which accords with conclusions revealed by other students of the region.

(b) *Beaches, Bars and Tombolos*.—From the cutting back of the cliffs and the stripping off of the glacial debris there was such an amount of material available that it could not be entirely carried off by the waves; some of it was deposited along the shore.

The most common features of marine deposition on Mount Desert Island are the fine bayhead beaches. At the head of nearly every cove we find these smooth, regularly curved gravel banks. The material varies in size, but is mostly composed of gravel; pure sand beaches are exceptional. If the supply of material is abundant, and the cove is not too much exposed to wave attack, the beach "progrades" or grows out toward

the sea. This is commonly the case on the Island, but where the material is scanty and the waves have easy access to it, we have "retrograding" beaches, such as Little Hunter's Beach, with a freshly cut cliff at head of the Bay.

(c) *Spits and Bars*.—These are formed when an oversupply of material, carried by the longshore currents, is built out into the water from the sides of the headlands in the form of a narrow sand-ridge.

Spits occur where the sand-ridge does not reach the next headland but terminates in open water. The best examples are between the two Cranberry Islands, where spits start out from both of the islands, but fail to join, leaving Cranberry Harbor still somewhat open.

Bars are formed when the sand-ridge almost or entirely closes the bay. They are usually concave toward the sea and often have an opening for the inflow and outflow of tidal waters. According to the width and depth of the bay, the nature of the longshore current, the available load,



FIG. 42.—Sandy Beach (Newport Cove) from the Beehive

the bar may be at the mouth of the bay (as on Long Pond*); in the middle of the bay (as in the submarine bar in Otter Creek Bay); or it may be driven back into the bays so deep that it actually reaches the bayheads, as in Hunter's Beach and Sandy Beach (Newport Cove), where the rivers behind the bars are ponded, forming fresh water pools (Fig. 42). Behind the bars stream deposition helps to fill up the coves.

* The pond here referred to is the lesser Long Pond at Seal Harbor, not the Long Pond mentioned elsewhere as among the major lakes of the Island.

(d) *Cusate Bars and Tomolos*.—When a bar forms a V enclosing a lagoon or marsh, it is called a cusate bar. The best example of a cusate bar is at Rice Point, on Sutton Island. When a bar connects an island with the mainland or with another island, it is called a tombolo, or island-tying bar. Tombolos are very common about Mount Desert Island. The name "Bar Harbor" is derived from a tombolo which connects Bar Island with the mainland. Nearly all the tomolos are flooded at high tide. A complex arrangement of bars, spits and tomolos may be noted around the Cranberry Islands.

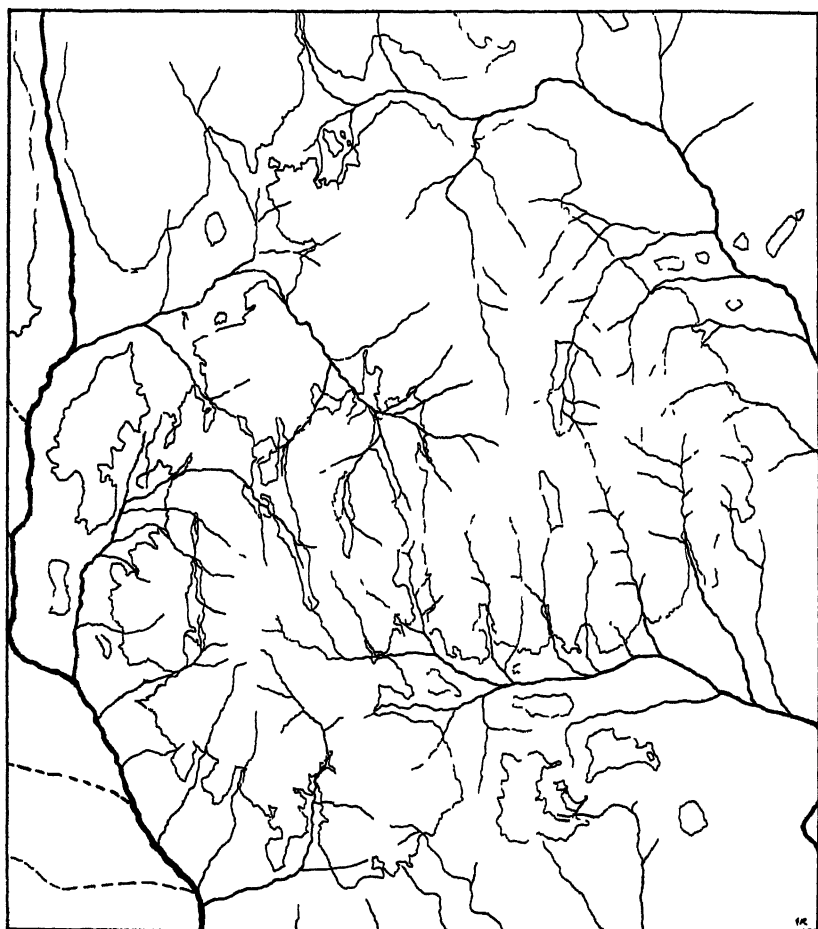


FIG. 43.—The supposed pre-glacial drainage of Mount Desert Island.

THE DRAINAGE HISTORY

For better understanding of the drainage problems on Mount Desert Island, the writer has attempted to reconstruct the river system of the Island as it appeared before the Ice Age. Map Fig. 43 shows the result of this study.

The map is based on the following assumptions:

- 1) The pre-glacial drainage was somewhat dendritic in pattern, but due to the structures in the granite had a noticeable N-S trend. It was in a mature stage of development.
- 2) The ice deepened and straightened the N-S valleys; the E-W valleys were in general unaffected, except that their north sides were made steeper and the southern walls smoothed.
- 3) The ice cut through the mountains deep glacial troughs, thereby establishing new drainage routes.
- 4) Each of the troughs represents a saddle in the pre-glacial crest, between the head-waters of north-flowing and south-flowing streams.
- 5) The pre-glacial crests of the mountains were pushed slightly southward during glaciation (see Fig. 44).
- 6) The deepest pre-glacial saddles were not necessarily at the place of the deepest troughs. The ice deepened most those troughs that were not too closely spaced; the others are represented only by smaller glacial notches.
- 7) The region was depressed during the last stages of glaciation several hundred feet under sea level. At the present time the region is still in a state of submergence, and the main streams are drowned.
- 8) In places where glacial erosion was most vigorous due to convergence of ice streams or to other causes, the ice carved basins which are filled with lakes at the present time.
- 9) Accumulation of glacial debris blocked certain pre-glacial stream channels to form lakes or swamps or even displaced streams to new courses.

A comparison of maps, one showing the pre-glacial drainage, the other the present drainage, discloses the marked changes introduced by glaciation and change of level. The pre-glacial drainage was well organized, while the present drainage shows disarrangement and abnormal conditions throughout.

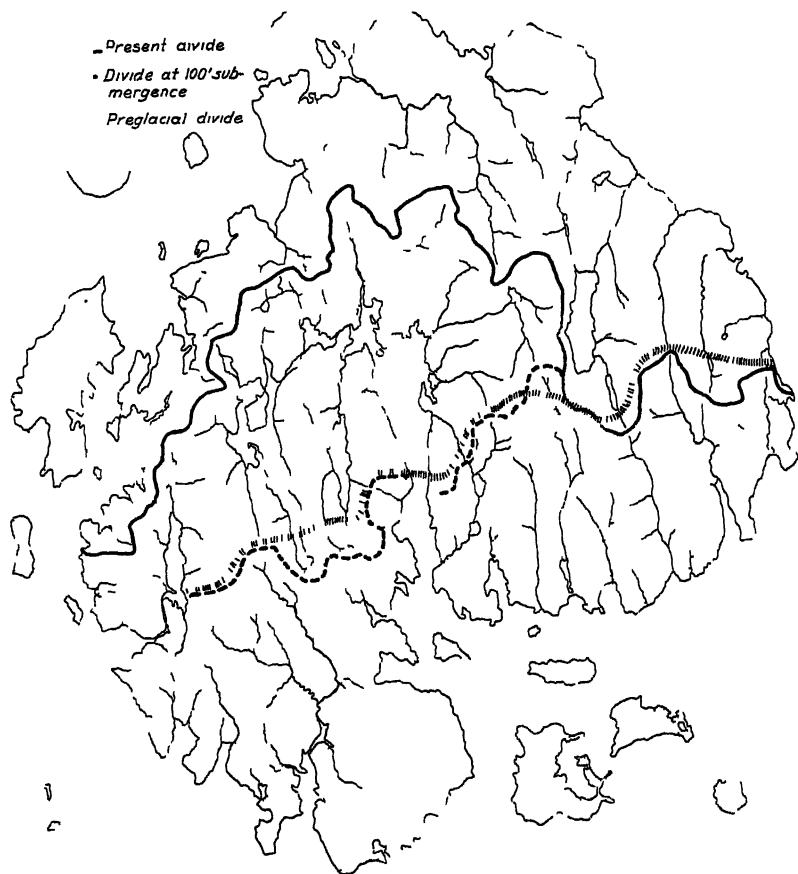


FIG. 44.—The shift of the divide on Mount Desert Island. The present divide is pushed far northward by the incision of *Somes Sound*. If the Island should be submerged 100', *Somes Sound* would cut the Island in two. The divides on the resulting two islands would be much nearer the former position at the crest of *Mount Desert* range.

THE DIVIDES

Fig. 44 shows the pre-glacial divide as compared with the divide of the present time. The most striking fact brought out by the map is the extreme irregularity of the present divide, illustrating the disorganized state of the present drainage. Before the Ice Age the divide was where it belonged, at the crest of the *Mount Desert* range. The present divide is on the crest only at one point; everywhere else it lies far to the north as an indistinct line not readily perceptible in the topography.

The northward transfer of the divide is rather accidental; it is the result of the presence of *Somes Sound*, which is cut straight through the mountain range and which at its northern end collects all the waters from behind the mountain. It is interesting to note that, if *Somes Sound* should cut the Island in two—as it nearly does—the divide on the islands so formed would be much nearer the normal position than is the present divide.

THE LAKES

Lakes are characteristic features of the young stage of drainage development, and especially so on a glaciated surface. There are about forty lakes on this relatively small island, and besides these a great many swamps, some of which represent filled-in lakes. The lakes belong to several types, and may be classified according to their origin.



FIG 45 —Glacial trough south of Bubble Pond.

1. LAKES OCCUPYING THE BASINS OF OVER-DEEPENED GLACIAL TROUGHS

Glacial troughs are former channels of ice streams, and like ordinary river channels they have uneven bottoms. The bottom is deepest in places where the channel passes through narrows in the mountains. As

the ice melted away, lakes were left in the basins. To this type belong the most beautiful lakes of the Island, as the Tarn, Jordan Pond, Bubble Pond, Echo Lake, Long Pond, Seal Cove Pond and Hodgdon Pond. Somes Sound would belong to this type but for the fact that it was carved below sea level and is now filled with salt water. If the land were to rise 50 feet, it would be converted into a lake like the others.

Most of these lakes are not exactly in the middle of the mountain belt, but appear to have been pushed rather northward. This was caused in part at least by accumulation of glacial debris at the southern outlets of the glacial troughs.

2. LAKES OCCUPYING FLAT BASINS NORTH OF MOUNT DESERT RANGE FORMED BY OVER-DEEPENING OF THE ICE WHICH CONVERGED BEFORE ITS ENTRANCE INTO THE MOUNTAINS

The formation of these basins is similar to that of the previous type. More ice needs a deeper channel and carves deeper at the bottom. The difference is that, in this case, the ice was not yet closely confined by mountain walls on both sides, and so made broad and shallow depressions. Accumulation of till may add to the ponding, but these lakes are essentially rock-carved basins, and would exist even if no till were present. To this type belong Aunt Betty's Pond; the pool north of Champlain (Newport) Mountain; the northern part of Long Pond and Echo Lake can just as well be classified with this type. Eagle Lake is transitional between the first and second type.

3. LAKES AND SWAMPS FORMED IN THE SMALL TROUGHS AT THE NORTH END OF THE GRANITIC LOWLANDS

To this type belong Lake Wood, and a number of swamps. The origin of the basins is the same as in the case of the large glacial trough lakes, but they are on a smaller scale. As the continental ice sheet ascended from the northern weak rocks upon the lower rim of the granitic lowlands, it utilized the N-S valleys, and deepened them to form miniature glacial troughs the over-deepened portions of which constitute lake basins.

4. LAKES DAMMED BY ACCUMULATION OF TILL

This condition is chiefly responsible for the string of lakes from the northern edge of Long Pond to Somes Sound. Most of these lakes are kept at their present level by artificial dams. A number of swamps originated as lakes of this type which are now drained or filled, as those north of Somes Sound.

5. LAKES DERIVED BY DAMMING THE OUTLETS OF RIVERS BY WAVE-BUILT BARS

Lakes of this type are found at Sandy Beach (Newport Cove) and at Hunter's Beach Cove, on the southern shore, as described in the previous chapter (see Fig. 42).

6. SADDLE LAKES

Lakes of this type occupy small depressions in the saddles of the mountains, as the Bowl, Saddle Lake on Cadillac (Green) Mountain, etc. The origin of the saddle lakes has already been discussed. They are rock basin lakes excavated in glacial spillways by the ice which passed through the saddles in a W-E direction from one glacial trough into another.

7. LAKE MAINTAINED BY BEAVER DAM

There is one little lake which is held in place by a dam built by beavers at Duck Brook, west of Great Hill. This dam is about 150 feet long and 6 feet high, and the water held by it is of considerable volume.

There are extensive swamps in the weak-rock belt, as the North-Eastern Branch swamp in the north, and Marshall Brook swamp in the south. Actually they do not belong in the group of lakes; they are shallow bays of the sea which are now partially filled up.

POST-GLACIAL STREAM NOTCHES

Not only have the young streams carved deep gorges in the soft glacial debris; they have attacked locally the granite bedrock itself. Kebo Brook, between Cadillac (Green) Mountain and Flying Squadron (Dry) Mountain, and the brooks on the northern flank of Sargent Mountain, have carved into the granite post-glacial notches which in places are 50 feet deep. The big boulders in the bed of the brook are the tools with the aid of which this relatively small stream accomplished its work. The main joint-system of the granite helped to determine the remarkably straight and vertical side walls of the notches.

DRAINAGE MODIFICATIONS

Bascom (4) has described a series of stream captures on Mount Desert, and Johnson (21) has expressed some doubt as to the correctness of her interpretations. A specific case studied by the writer concerns Aunt Betty's Pond. Bascom (4-p. 128) assumes that this pond, which occupies a broad, shallow rocky basin, drained first to the north, and later was captured by Richardson's Brook, which enjoyed the advantage of a shorter and steeper descent to the sea.

Although the map strongly suggests this explanation, the writer questions its validity. The region of Aunt Betty's Pond probably did drain to the north in *pre-glacial* times, but it is highly improbable that there was a lake there at that time. When the region was glaciated, the ice excavated a broad shallow basin at this place. As the ice melted, water filled the basin and overflowed to the south, as the ice presumably still blocked the pre-glacial channel to the north. The pre-glacial channel is

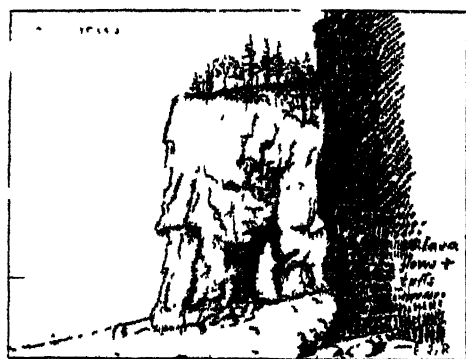


FIG 46 —A marine arch at The Ovens.

visible north of the lake, but there is no notch in the divide which would indicate that the lake had an outlet in post-glacial time in this direction, or that capture had taken place in the manner suggested by Bascom.

FUTURE DEVELOPMENT

The unbalanced condition of the present drainage cannot last long. The streams will cut down their barriers and fill up the basins. The lakes and swamps will thus disappear, as many of the former lakes and swamps have already done. The streams will clean out their valleys, carrying off first the unconsolidated glacial material. Later they will cut into the bedrock, widen their valleys, and if uninterrupted in their work, will finally level down the land to a nearly flat peneplane, unless the sea waves first sweep away the Island. The granitic mountains were able to withstand peneplanation during at least one long erosion epoch, and survived as monadnocks. If a similar long erosion epoch should now follow, they would not be so well able to survive because of their dismembered condition caused by glaciation.

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